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Social structure, activity budgets and spatial relationships of the British & Irish captive population of lion-tailed macaques (*Macaca silenus*).

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ABSTRACT

Less than 2500 mature lion-tailed macaques (*Macaca silenus*) are left in the wild in the Western Ghats, India. It is important to manage and sustain the captive populations to gain an insight into this species and how to manage the wild fragmented populations. The European captive population suffers from high infant mortality, large birth intervals and a low reproductive success amongst females. Thus the aim of this study was to assess possible causes of these three factors by investigating the social structure, activity budgets and spatial relationships in the captive British and Irish population of lion-tailed macaques. Observations were carried out at all zoos housing this species in the U.K. and Ireland. Observations were made over 12 days per zoo at 09:00h, 12:00h and 15:00h. The average distance between individuals within a group was determined using Animal Tracker® computer software. Activity budgets were constructed for each zoo. Enclosure size, enclosure complexity, feeding regimes and visitor numbers were investigated to determine any influence on spatial separation distances and activity budgets. The social structure varied between groups due to age, sex and number of individuals and the facilities surrounding each of the groups. The degree of relatedness between females, as well as the size of enclosure, appeared to influence the spatial separation distances between individuals, although not significantly. The activity budgets varied between zoos, with autogrooming and foraging showing significant differences throughout all sampling periods. Significant differences in behaviour were also found between adult and juvenile lion-tailed macaques and in relation to time of day. Visitor numbers and feeding regimes appeared to have no effect on the macaques' behaviour. However, enclosure size and enclosure complexity did appear to influence behaviour. In conclusion, this study of captive lion-tailed macaques gives an insight into how wild fragmented populations may be influenced by a reduced and isolated habitat. This study will also provide information regarding the welfare of captive lion-tailed macaques.

CHAPTER 1. INTRODUCTION

1.1. GENERAL INTRODUCTION

Many species of animals are now facing high risks of extinction in the wild due to the increased pressures from habitat destruction, predation and disease. Habitat destruction in particular causes populations to become fragmented, thus allowing subpopulations to form with a low genetic diversity, leading to a lower chance of adapting and surviving in new environmental conditions. As a result, sample populations are being represented in zoos and participating in captive breeding programmes in order to prolong the survival of endangered species.

In some cases, the reintroduction process of captive bred species has been successful; examples include the re-introduction of the Harvest mouse (*Micromys minutus*) in Chester, U.K. and the re-establishment of Siamese crocodiles (*Crocodylus siamensis*) in Cat Tien National Park, Vietnam (IUCN, 2003). However, there are many reintroduction programmes that have proven to be unsuccessful or proved to be very problematic in the early stages, as a result of the species being unable to adapt to a new environment due to the lack of suitable, protected habitats required in order to establish such programs.

Also, it was found that some reintroduced species lack appropriate life skills in order to adapt to life in the wild, an example of this is the golden lion tamarin (*Leontopithecus rosalia*). The first reintroduction programme of this species identified that reintroduced zoo-born tamarins showed deficiencies in the identification of feeding, locomotion and orientation in their new environment. A major loss of reintroduced tamarins was through theft and vandalism by humans and there was an inverse correlation between age at release and post-release survival. Thus it was concluded that family groups were the best unit for reintroduction and a development of a combination of pre- and post-release training as the most cost-effective method of reintroduction for this species. Also, an increased effort was placed on educating the local Brazilian landowners, citizens,

political leaders and teachers regarding how endangered the golden lion tamarin is and why it needs to be protected. Through this conservation program there are now 1200 golden lion tamarins living in the wild and thus although this reintroduction programme was problematic at first, it is now one of the most successful reintroduction programmes to date (Smithsonian National Zoological Park, 2004).

Primate species inhabiting fragmented regions of a tropical forest face several ecological constraints, such as restricted home ranges, low tree densities, low food availability, high predation risk, and increased hunting pressure. These constraints consequently impinge on the diet, mortality rates, reproductive rates and ultimately survival of the species (Menon & Poirier, 1996). Therefore, in order for reintroduction programmes to be successful, these ecological constraints need to be addressed and improvements have to be made to ensure that a species can enter a sustainable environment.

Captive populations, in a sense, could be used as models for severely fragmented populations and could provide quasi-experimental and experimental conditions that would be difficult to establish in the field (Kaumanns *et al.*, 2001). In the wild, it is hard to monitor a continuously moving primate population over a short period of time, particularly when populations are so fragmented. Predators that are dangerous both to man and the focal species can obviously disrupt field experiments along with adverse weather conditions and other environmental factors. These factors have a lower or no influence in captivity. Thus, there is a need to correlate research that occurs in zoos with that which takes place in the wild, so that successful management plans can be formed enabling viable populations to remain or to be reintroduced and survive in the wild.

1.1.1. The lion-tailed macaque (*Macaca silenus*)

Lion-tailed macaques (*Macaca silenus*) belong to the family *Cercopithecidae* and are among the smallest, most timid and most arboreal species belonging to the genus *Macaca*. Due to habitat degradation the species is facing several ecological constraints

and thus is struggling to survive in the wild (Singapore Zoological Gardens Docents, 2000). Lion-tailed macaques are said to be the direct descendent of the first macaque to reach Asia (*M. paleoindica*), nearly 5 million years ago (Kumar, 1995b). Environmental changes during the Pleistocene, i.e. changes in the glaciation and the monsoonal climate, isolated the ancestral stock to the Western Ghats, India, whereas the stock that had reached Southeast Asia underwent repeated speciation (i.e. the evolutionary process by which one species arises from another), to give rise to most of the extant macaques (Kumar, 1995b). Lion-tailed macaques have been classed as an old world monkey, due to characteristics such as lacking a grasping tail, having close-set nostrils and more opposable, grasping thumbs (Hickman *et al.*, 1997).

In the past, the lion-tailed macaque population was distributed as a continuous population from the southern end of the Western Ghats to the state of Maharashtra. The Western Ghats are geologically split into two areas separated by a 40km 'Palghat' gap that naturally divides the northern and southern populations of lion-tailed macaques (see Figure1). Within this area, there has been an increase in logging, agricultural expansion, commercial plantation and the development of water conservation schemes for power generation (Singh *et al.*, 2001). More recently, this macaque's distribution range in the north, has shrunk to just north of the Sharavati River in Karnataka. Due to the lowland rainforests in Kerala and Karnataka being destroyed, the population of lion-tailed macaques has been confined to higher elevations (Kumar, 1995b). Thus, the forest has now become very much fragmented and as a result the lion-tailed macaque population has been forced to divide into small breeding populations (Singh *et al.*, 2001) (see Figure 1).

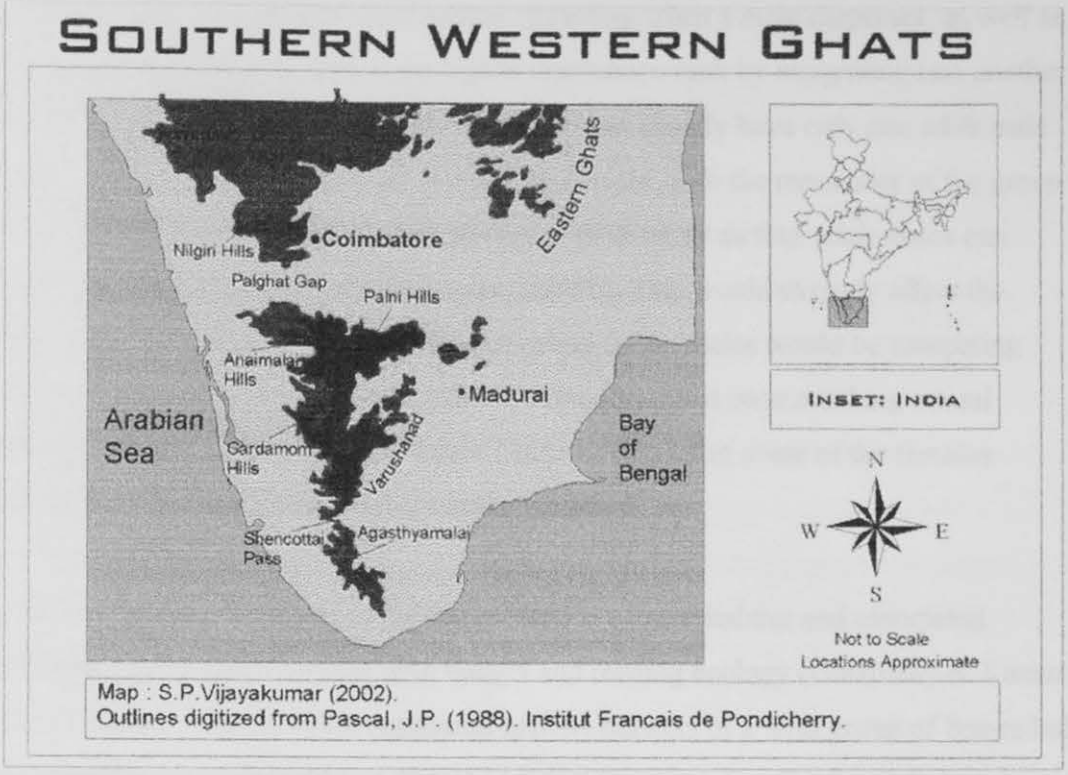


Figure 1: Map showing the Western Ghats, India which the lion-tailed macaque (*M. silenus*) is endemic to.

1.1.2. Social structure and activity budget

The lion-tailed macaque lives in groups with an average of approximately 16 animals. In undisturbed habitats, the group size ranges from seven to approximately 40 individuals, however, in forest fragments such as in the Anamalai Hills (see Figure 1), group size can be as high as 65 animals (Kumar, 1995b). This is a 'female bonded species', whereby the females remain in their natal nest and the males emigrate once reaching adolescence at 8 years of age. These macaques can live for up to 20 years in the wild and may live 30 years or more in captivity (Woodland Park Zoo, 2000). There have been many suggestions regarding why males disperse from the group (Ananda Kumar, 2001). Incest avoidance appears to be the most important causative factor for male dispersal (Shields, 1987). However, competition among males and access to more estrus females (Alberts

& Altmann, 1995) would have implications regarding when a male disperses, as well as the possibility of the male obtaining a higher dominance rank by emigrating into another group (Borries, 2000). In undisturbed forests, groups usually have only one adult male with six or seven adult females and one sub-adult male, with the remainder of the group being immature individuals. However, groups with as many as four adult males can occur in disturbed forest fragments (Kumar, 1995b). This would strongly affect the success of reproduction within the macaque group as the males would be competing against each other and as these males should have dispersed once reaching sexual maturity, it is most likely that these males would be related to some of the females meaning there is a risk of inbreeding within the group.

The first responses of animals to the fragmentation of their habitat and associated disturbances are changes in their time budget and feeding ecology (Umapathy & Kumar, 2000). Menon & Poirier (1996) compared activity budgets of a feral group of lion-tailed macaques that were confined to a disturbed forest fragment, (i.e. the forest fragment was surrounded by tea and coffee plantations or heavily used roads) with activity budgets of groups in protected forests. They found that in the disturbed forest fragments the groups spent the largest proportion of time each day ranging (34%), which was defined as directional travel and includes movements from one canopy level to another (vertical travel) or over long distances (horizontal travel). The second most common activity was foraging (23.7%), defined as an active search for and selection of food items. Feeding (17.9%), defined as the actual manipulation or intake of food items was the third most common activity and resting (16%), defined as inactive sitting or standing was the fourth. In protected forests however, the macaques spent only 15% of their time ranging, with resting (27.8%) and feeding (27.8%) being the most common activities, followed by foraging (26.7%). One probable cause for these observed differences in activity budgets between protected and disturbed forests is the fact that food availability emerged as a key influence on time budget. If more food is available in close proximity to the macaques' range, thus do not have to travel far to forage, thus more time can be allocated to other activities such as resting (Menon & Poirier, 1996).

The diet of the lion-tailed macaque consists of plant parts (mostly fruit, flowers and seeds), animals (mostly invertebrates), and other items (mushrooms and lichens) (Umapathy & Kumar, 2000). This species, as well as being classed as a habitat specialist due to occupying solely the rainforests of the Western Ghats (Singh *et al*, 1997), is also classified as a frugivorous or faunivorous species, with a bimodal dietary strategy as it feeds on both fruit and fauna (Kumara *et al*, 2000). Feeding in the day usually includes two major feeding bouts, often on large food trees such as *Cullinea exarillata*, several species of *Ficus* and *Artocarpus heterophyllus*. *Cullinea exarillata* and *Ficus* species are the keystone resources for lion-tailed macaques. It was found that these important keystone species, which are aseasonal in fruiting (*e.g. Ficus* spp.), or provide flowers and fruits over long periods of time (*e.g. Cullinea exarillata*) have been left intact in forest fragments since they are not of commercial importance. Compared to contiguous, undisturbed forests, small fragments appear to have a greater proportion of food trees. Other vegetation, such as coffee plantations, orchards of Mangos, Jack fruits, Guava and so on, surround these forest fragments and provide an additional food resource which many lion-tailed macaques spend time feeding (Umapathy & Kumar, 2000). In Menon & Poirier's (1996) study comparing the activity budgets between groups occupying a fragmented forest and a contiguous, undisturbed forest, the time budget was compressed during months when these key resources were not fruiting, because additional time devoted to foraging was at the expense of resting.

Lion-tailed macaques have a propensity for arboreality, making neighbouring forest fragments inaccessible to groups confined to isolated fragments (Menon & Poirier, 1996). It has been observed that lion-tailed macaques migrate between groups with interconnected forests (Kumar, 1987), however, they have not been observed crossing large gaps between forests separated by cultivation or human habitation. These populations would consequently become geographically and possibly genetically isolated and thus become inbred due to no immigration or emigration of males. This in turn could decrease the fetal, neonatal, and juvenile survivorship, lower competitive ability and lower fertility in inbred populations. The potential therefore, for the group to

adapt to environmental changes declines, which obviously has implications for the survivability of this species (Menon & Poirier, 1996).

1.1.3. Group encounters and spatial separation

In primates, inter-group encounters are relatively frequent and the interactions involved are often highly variable, from friendly interactions to aggressive confrontations (Cheney, 1987). Wrangham (1980) suggested that female-bonded species such as macaques should follow the 'resource defense hypothesis'. This is where females are expected to be hostile towards females in other groups over food resources as their reproductive success is potentially reduced by inter-group competition. This does appear to occur in lion-tailed macaque societies (Kumar & Kurup, 1985). Kumar and Kurup (1985) observed females showing aggression towards members of neighbouring groups and they were not seen to exchange friendly behaviour across groups.

Obviously the reproductive success of males depends largely on their access to fertile females and their ability to monopolize them (Zinner *et al*, 2001). This is where the theory of a 'mate defense hypothesis' has been formed. During intergroup encounters, males may either try to gain access to females of another group, to exclude other males from access to females of their own group (mate defense hypothesis) or both. Females will attempt to defend their dominant male from any females trying to enter their group and thus retain their position within the group. In Zinner *et al's* (2001) study of experimental inter-group encounters in lion-tailed macaques, they found that when individuals from an existing group were added to a larger group, the male leading this larger group directed aggression towards the extra-group female and male. However, when comparing this with the reactions of a male in a smaller group to added members, little aggression was shown. This indicates that possibly the male in the larger group may feel more threatened to immigrant individuals compared with the male leading the smaller group. Males in both groups were also observed herding their females aggressively and mounting them more frequently during encounters with other groups.

However, in the wild no aggression or friendly behaviour between males of different groups was observed by Kumar and Kurup (1985). This study, however, showed that males chase and threaten females of neighbouring groups and in turn, females were observed threatening and chasing extra-group males i.e. young males that had dispersed from groups and formed bachelor groups.

In the wild, lion-tailed macaques forage individualistically, thus there is a high spatial separation distance between individuals within the group (Green, 1978; Johnson, 1985). Adult males in particular have been observed to have a low rate of interaction with other group members and often remain on the periphery of the group (Hohmann, 1988). It has also been observed that females and their young tend to avoid being near to males when the troop is aggregated in fruiting trees (Green, 1978). Differences in spatial separation and consequently behaviour would be expected in captive populations compared to wild populations due to a much diminished territory size. For example, in captivity, individuals are forced closer together due to small enclosures, meaning that the frequency of behaviours such as aggression would be predicted to be higher, as individuals cannot escape tense situations. This would be evident particularly in a feeding situation when although enough food is provided for all individuals within the group, young individuals may try and compete with dominant individuals to gain access to preferred food.

As well as spatial separation distances between individuals within a group and between neighbouring lion-tailed macaque groups, lion-tailed macaques also share their habitat with a threatened species the nilgiri langur (*Presbytis johnii*). When two species compete for limited resources, the study of sympatric species, particularly endangered species, can provide information on feeding substratum, food items, and activity patterns which may help design scientific conservation and management strategies (Singh *et al*, 2000a; Kurup & Kumar, 1993), as well as give an insight into the adaptive processes leading to niche selection (Fleagle, 1988). Singh *et al.* (2000a) found that these two sympatric species of primates specialise on different food resources, but resource competition

occurs, the lion-tailed macaque appears to be the dominant species, as the nilgiri langurs shift their feeding to a lower substratum. Nilgiri langurs tend to depend on lion-tailed macaques to gain access to *Cullenia* fruits, the langurs favoured food. The lion-tailed macaques can easily open the hard outer case of this fruit using their teeth, however, it is not possible for langurs to open them thus, they have to wait until the seeds within the fruit are dropped from the hands of a lion-tailed macaque (Singh *et al.* 2000a). Therefore, these species can co-exist in the same habitat. However, if further degradation occurs, competition for resources would increase between the two species.

1.1.4. Reproductive history

From studies in the Anamalai hills, Western Ghats (see Figure 1) where lion-tailed macaque groups have been studied for over a decade, it has been recorded that this species has a very low birth rate (the proportion of females giving birth in a year) compared to most other macaque species. Data from eight groups gave a birth rate of only 0.30 (SD = 0.07) i.e. out of eight groups, only 30% of females gave birth in a year. Consequently, the inter-birth interval is long, where data from three females in this study area gave a mean of 30 months with a gestation length of approximately six months (Kumar, 1995b; Lindburg, 2001). From studies of the wild population, it has been recorded that the average age at which females give birth for the first time is six years, which is unusually high compared to other macaque species. One redeeming aspect of the lion-tailed macaques' reproductive history is that they seem to have a very low mortality rate of only about 5% (0.05/year) for all age/sex classes together. Adult males, however, do have a greater mortality and emigration rate of 8% (0.08/year) compared to adult females of only 3% (0.03/year) due to their tendency to migrate after reaching adolescence. These life history parameters (high age at first birth, low birth rate, long inter-birth interval and low mortality rate for all age/sex classes) are considered to impede the lion-tailed macaques' ability to adapt to changes in resources and to recover from population disturbances such as disease or hunting (Kumar, 1995b).

Female lion-tailed macaques have a pronounced phase of sexual skin tumescence, which indicates to the male that she is in oestrus. She also emits a characteristic staccato call during most copulations (Lindburg & Harvey, 1996). The duration of the sexual cycle is on average 30 days with a swelling phase of 14 days and a flat phase of 16 days. Mating reaches a peak about 11-13 days after the swelling appears (Kumar, 1995b). Lion-tailed macaque males are possibly mixed mount ejaculators. Thus they will often ejaculate during single mounts but will more likely ejaculate during multiple mounts, however, the frequency of either could change with successive days of sexual swelling (Kumar, 2001).

This species breeds non-seasonally in the wild and this is also true for the captive population. It has been reported, however, that reproductive synchrony occurs in captive lion-tailed macaques. It was found that the majority of births occurred in cohorts consisting of 2-5 infants being born within a three-month period. This synchrony may be a result of female competition. As males are a limited resource in captivity and possibly also in the wild fragmented populations, when males are available, females will compete to gain access to that male (Harvey *et al*, 1991).

1.1.5. Conservation status of lion-tailed macaques

The remaining wild population of lion-tailed macaques was assessed by IUCN (International Union for Conservation of Nature and Natural resources) in the 1970s. In the 1990s it was estimated that there were only approximately 4000 lion-tailed macaques left in the wild (Easa *et al*, 1997). This has now decreased to around 2500 mature individuals and consequently lion-tailed macaques are now listed as endangered on the IUCN red list. Thus, they are facing a very high risk of extinction in the wild in the near future (IUCN, 2003).

As a result of such low numbers being recorded in the 1970s, American zoo biologists in particular developed management strategies and a species survival plan (SSP) to

establish a captive population, which could act as a reserve and a model for the highly threatened wild population. Following on from this, in 1989 a European endangered species programme (EEP) for lion-tailed macaques was established. Twelve institutions signed up at the start of the programme and by 1999, 33 institutions had joined. The result of this programme was that the number of individual macaques in captivity grew from around 90 in 1989 to around 200 by the end of 1998 (Kaumans *et al*, 2001). At the end of 2000, the European captive population of lion-tailed macaques constituted about one third of the global captive population and almost 5% of the total number of lion-tailed macaques both in captivity and in the wild. In 2001, the size of the European population did not increase (Krebs & Kaumanns, 2002), however in 2002 it increased by 7%, thus 236 individuals now comprise the European population, distributed among 41 colonies (Krebs & Kaumanns, 2003).

1.1.6. Problems within the captive population

The life history patterns, for example, the birth and mortality rates, dispersal patterns and generation time in the European population of lion-tailed macaques and possibly in the Indian and American populations do not resemble the patterns in natural populations closely enough (Krebs & Kaumanns, 2002). The main problems are high infant mortality, a low number of births that fluctuates from year to year, a significant proportion of adult females do not breed and slow population growth, thus posing the risk of significantly reducing genetic diversity (Krebs & Kaumanns, 2003). During the period of 1989 to 1997, out of 35 females capable of reproducing, only 12 or 34% gave birth. This means that almost 50% of the European Endangered species Program populations reproductive output, was generated by only about one third of this population and this appears not to have changed (Kaumanns *et al*, 2001). For example, the infant mortality rate in relation to the total mortality rate of the captive population was high at 36.4% in 2001, with about 28% of the approximately 75 reproductive females giving birth in 2001 (Krebs & Kaumanns, 2002). Overall for the period between 1950 and 2000 it was found that 50% of the 203 females (>4 years, i.e. born before

1996) of the European lion-tailed macaque captive population did not reproduce during their lifetime or to date. The figures show that 2.9% of the females gave birth once, but the infants did not survive and only 47.4% of the females gave birth to at least one surviving infant (Kaumanns *et al*, 2001). This obviously has strong implications on the rate of population growth, which is why only a 7% increase in the captive population was observed in 2002 (Krebs & Kaumanns, 2003).

Most institutions involved in the European Endangered species Programme population can only keep single male with multi female groups and few all-male groups exist, meaning that a large number of subadult and adult males have to be kept separately from the breeding units. Also, many groups in the population do not have as many adult females in comparison to wild groups, which normally comprise on average 16 individuals. This leads to untypical social structures, as strong matrilines cannot form and grow into clans (group of related females) of an appropriate size. If large enough clans were formed then large groups could be divided to form new groups, in which surplus males could be introduced (Krebs & Kaumanns, 2002). The age/sex composition of the population was a problem in 1997, as it was biased towards adults and in particular towards individuals that were more than 15 years old (Kaumanns *et al*, 2001). This still appears to be true in the current European population, where there is a greater proportion of females aged 11 years or more (Krebs & Kaumanns, 2002). As long as reproductive success remains low, the captive population will not be able to increase at a steady rate.

When carrying out behavioural studies on captive lion-tailed macaques most individuals are said to be "looking fine and doing well" (Kaumanns personal communication, 2003) however, there is almost no colony that lacts few individuals expressing subtle behavioural disturbances such as saluting (hand to eye movements, see Chapter 4) or other types of stereotypic behaviour. The subtle nature of the abnormal behaviours makes it difficult to assess the actual extant of the problem within the captive population as a whole (Kaumans *et al*, 2001). However, these behaviours are possibly only

exhibited by a few individuals in relation to the size of the captive population, which may mean that the majority of the population has the ability to adapt to a captive environment.

1.1.7 Welfare of captive primates

Welfare is obviously one of the key issues when analysing the behaviour of captive animals. The behaviour of an animal can give an indication regarding the health of that animal (Dawkins, 2004). Species vary in their responses to potential threats to welfare. For example, when various rodent species are placed in a novel open arena, all show behavioural signs of stress, but guinea pigs (*Cavia porcellus*) tend to become immobile, while chinchillas (*Chinchilla laniger*) move actively around the arena, biting objects within it and defecating extensively (Glickman & Hartz, 1964). Even very closely related taxa may differ, for example, crab-eating macaques (*Macaca fascicularis*) show greater corticosteroid responses to novelty or restraint, greater and more prolonged increases in heart rate in response to a novel environment, and more alarm-calling when disturbed by humans, than do bonnet macaques (*Macaca radiata*), while these in turn show a higher response compared with rhesus macaques (*Macaca mulatta*) (Clarke & Mason, 1988; Clarke *et al*, 1994). Thus, species vary greatly in the nature and magnitude of their responses to captivity, which can be a practical problem when trying to understand and improve animal welfare (Clubb & Mason, 2004).

Many zoo animals are said to show signs of stereotypy, thus exhibiting unvarying, repetitive behaviour patterns that have no obvious function or goal and possibly provides evidence for specific behavioural restriction or deprivation (Petherick & Rushen, 1997). This hypothesis has been demonstrated in primates where stereotypic behaviour was reduced by up to 73% in macaques by introducing a 'fleece pad' to encourage grooming and also introducing a fleece pad sprinkled with foraging crumbles to induce foraging activities (Lam *et al*, 1991).

The environment will obviously have an effect on the behaviour of captive animals, which is one of the main reasons why so many zoos now focus on environmental and social enrichment. Newberry (1995) defines environmental enrichment "as an improvement in the biological functioning of captive animals resulting from modifications to their environment". Evidence of improved biological functioning could include increased lifetime reproductive success, increased inclusive fitness or a correlate of these, such as improved health (Newberry, 1995). Enrichment procedures are designed to promote natural behaviours such as grooming, foraging and play behaviour over intervals of weeks and months (Schapiro *et al*, 1996). Thus, environmental enrichment is said to have been carried out, when a captive animal's environment has been changed, by adding a new stimulus with the intention that it will create a positive effect on that animal's behaviour.

It has been shown that social primates such as rhesus macaques benefit greatly from added social enrichment. The behaviour of singly, paired and group housed rhesus monkeys was compared and it was found that the social housing and/or age of subject significantly affected time spent inactive, grooming, playing, exploring and behaving abnormally (Schapiro *et al*, 1996). Social housing resulted in more species-typical behaviour patterns than did single caging and subjects were more socially orientated when pair-housed than when living in small groups. One of the most interesting findings from this study and probably the most important was that the presence of social partner(s) led to more beneficial changes in behaviour than did the provision of inanimate enhancements, such as feeding devices, thus concluding that social enrichment should be provided when possible and appropriate (Schapiro *et al*, 1996).

The appropriateness of social enrichment is particularly important when assessing the welfare of lion-tailed macaques. They are social primates and it is common for unfamiliar individuals to enter the group both in the wild and in captivity due to the frequent turnover of the dominant male. In the wild, the incoming male may spend time on the periphery of the group trying to build up relationships with members of the group

before actively competing with the dominant male of that group. However, in a captive situation there are strong implications for the welfare of both the individual male and of the group when changing the dominant male of a captive society. Thus, it is important to allow new males have to the opportunity to build up relationships with members of a new group before being actively housed with them (Mendl & Newberry, 1997).

There are many suggestions of ways to prevent individuals from adversely affecting the welfare of fellow group members. Animals should be provided with opportunities to avoid each other, thus reducing physical conflict and a managed environment should provide all group members with ways of obtaining resources without the need for competition (Mendl & Newbury, 1997). This should be one of the fundamental aims of all zoos and institutions that hold captive animals.

It is only recently that zoos are evolving more towards conservation resource centres or "wildlife conservation parks". These new institutions not only possess the traditional facilities for keeping and displaying wild animals (and the long-term propagation and educational programs that occur with them), but as environmental centres they also directly support *in situ* conservation programs by providing administrative, curatorial, editorial, financial, scientific and veterinary resources. This support is created, for example, by sending zoo-based personnel to work in the field, sharing animal and scientific facilities, donating money for *in situ* work and contributing animals for reintroduction (Koontz, 1997). More importantly there are more personnel employed by these institutions that assess the welfare of captive animals, and stronger legislations are now in place regarding how animals should be housed and husbandry procedures etc. It is a necessity, however that species are treated as separate cases when assessing welfare due to species-specific differences in reaction to stressful situations, as stated previously.

1.1.8. Relevance of this study

In assessing the status of the European population, it was recommended that large groups needed to be established, so that females could remain in their natal groups, as occurs in the wild (Krebs & Kaumanns, 2003). Male turnover, i.e. transfer of males between captive groups, would also be important, as it would create genetic variability within the population. However, both these recommendations prove to be difficult due to space limitations in zoos. This means that large groups are not able to be housed, and there is a risk of infanticide by transferred males. Most importantly, this would not solve the main problems of high infant mortality, large inter-birth intervals and low number of breeding females, that is so prevalent in captive lion-tailed macaque groups (Krebs & Kaumanns, 2003).

Little is known about how the social system operates in lion-tailed macaque societies as in the wild, long-term observations can be difficult due to various practical problems, for example, the dangers of passing elephants. If we could understand how the social structure is organized in the captive population with a low rate of male turnover, it might help towards understanding what occurs in the fragmented populations that occur in the wild. This would mean that the captive populations could act as a model for the fragmented populations (Kaumanns personal communication, 2003).

One of the main aspects for future studies on lion-tailed macaques is to analyse their reproductive biology and try and form recommendations about how to increase the reproductive success of this species (Kaumanns personal communication, 2003). An analysis of sexual swelling data from females revealed a significant decline in the duration of the tumescent phase (sexual swelling of the skin period) over a recent four-year study. One suggestion is that due to the absence of turnover of males in captive groups, there is an associated reduction of novelty for females in choosing males, which could in some way reduce the investment in advertising oestrus by females (Harvey & Lindburg, 2001).

In the wild, females will obviously be attracted to males that advertise the most beneficial characteristics, such as having a large body size, since they can compete and win against other males and most importantly defend their territory. If a new male tries to compete with the existing male and wins, obviously this male would be the best to mate with, as he has more favourable characteristics and will defend his group and territory well. This means that the females would then have to compete with each other to gain access to this male, which is where the dominance rank of the female would become important. A male will mate with females that have the most pronounced phase of tumescent (i.e. the largest swelling), as this advertises that she is at the peak of her oestrous cycle and thus most likely to conceive. Obviously the more a male mates with a particular female, the chance that she will become fertilized increases and thus his genes will be passed on. The infant would then take on the dominance rank of its mother and a hierarchy would begin to form and be maintained by the support of female relatives. Thus, if the male maintains this strategy and manages to defend his group from competing males, the rate at which his genes are passed on increases as the group size increases, which is obviously one of the main aims of a male in any society (McFarland, 1999). In captivity if there is no competition for the male, females do not need to advertise or compete as much as there is no external competition, thus probably reducing sexual tension within the group and maybe in turn affecting the reproductive success of the group.

Behavioural studies looking at copulatory behaviour, activity budgets and most importantly social interactions and spatial relationships within captive groups, would provide a valuable insight towards understanding how the social system and reproductive behaviour operates in captive or fragmented lion-tailed macaque groups. This would also provide indications of the welfare of this species in captivity. In turn, recommendations could then be formed on how to manage the captive population and fragmented wild populations to produce an optimal reproducing population.

1.2. GENERAL AIMS

The aims of the project were:

1. To analyse the social structure of five captive groups of lion-tailed macaques (*Macaca silenus*) by looking at the reproductive potential of groups and relationships within groups and relating this to other macaque societies.

2. To assess spatial relationships within captive groups and relate this to reproductive behaviour and success.

3. To provide a description of the activity budgets of captive lion-tailed macaques and relate this to the groups' social structure and enclosure design. To state the relationship between social and non-social interactive behaviours.

4. To assess how environmental factors such as enclosure complexity and feeding regimes influence the macaques' activity budgets.

5. To examine overall, how the composition of groups, in particular social relationships, social structure and interactive behaviours, would have an effect on the macaques' adaptability to a changed environment, thus relating findings in captive populations to isolated fragmented populations in the wild.

CHAPTER 2: GENERAL MATERIALS AND METHODS:

2.1. Animals

All British and Irish zoos and wildlife parks that housed lion-tailed macaques were used in the study with one exception, as this only had one male macaque. Thus, 37 individuals were observed in this study, divided between four zoos and one wildlife park (Zoos A, B, C, D and E) however, throughout this thesis the wildlife park will be referred to as a fifth zoo (Table 2.1). All zoos in this study were part of the European Endangered species Programme (EEP). The macaque groups varied in social structure, with some groups consisting of a dominant male, juvenile male and multi-females, whilst others consisted of multi-male, multi-female groups. The details of each zoo will be discussed in Chapter 3.

2.2. Background information

A questionnaire was sent out at the beginning of the study to each participating zoo to gain knowledge of housing and husbandry procedures (see Appendix 1). If a zoo did not return the questionnaire, the questions were asked on arrival at the zoo to gain the relevant information. The questions mainly asked were how many lion-tailed macaques were held at each zoo (see Table 2.1), the macaques' diet, if they received additional vitamin supplements, immunization etc and general questions regarding the enclosure size and layout (see Chapter 5).

Table 2.1. Details of study individuals. Individuals were classed as juveniles if they were four years and under.

Individual	Zoo	Sex (M/F)	Age (Years)	Adult (A) /Juvenile (J)
1	A	F	22	A
2	A	F	7	A
3	A	F	7 months	J
4	A	F	13	A
5	A	F	6	A
6	A	M	1	J
7	A	F	15	A
8	A	F	6	A
9	B	F	12	A
10	B	M	13	A
11	B	M	3	J
12	B	F	3	J
13	B	F	15	A
14	C	F	5	A
15	C	M	9	A
16	C	F	6 months	J
17	C	F	2	J
18	C	F	9 months	J
19	C	F	11	A
20	C	M	3	J
21	C	F	3	J
22	C	F	9	A
23	D	M	3	J
24	D	M	4	J
25	D	F	14	A
26	D	F	10	A
27	E	F	11	A
28	E	F	1	J
29	E	F	6	A
30	E	F	1	J
31	E	F	12	A
32	E	F	3	J
33	E	M	23	A
34	E	F	20	A
35	E	F	4	J
36	E	F	2	J
37	E	M	2	J

The diet of the captive macaques in all five zoos varied according to each zoo, but generally consisted of a combination of pellets, fruit, vegetables and other supplementary foods (Table 2.2).

Table 2.2. Lion-tailed macaque diet in captivity

Type of meal	Diet
Breakfast	Mazuri primate pellets or Old World monkey pellets.
Fruit and veg feed	Lettuce, carrots, spinach, broccoli, celery, apples, pears, oranges, grapes, bananas, cauliflower, bread, eggs, potato, pineapple heads, melon, strawberries (Any other main fruits that have been leftovers from supermarkets).
Extras	Live food (locusts, mealworms), Mixed nuts, parrot mix, sultanas Maize Browse – i.e. willow Zoo C – also sprinkled Ionate as a vitamin and mineral supplement. Novelty foods: honey sticks, pine cones, fruit branches, food puzzles, coconuts and natural fruits from trees in enclosure.

Some fruits are only seasonal such as melon and strawberries therefore the diet would vary throughout the year. The amount of food would be increased where pregnant females or young were present within the group (e.g. Zoos B and C). It was also found that some zoos provided baby food to lactating females to boost their energy and nutrition.

The variation in feeding regimes, types of enrichment and enclosure complexity will be further discussed in Chapter 5.

With regards to the health of the captive lion-tailed macaques, some zoos carry out regular faecal screening for parasites and tests for Herpes B (mainly Zoo D). However, since these are wild animals, individuals were only medicated when it was absolutely necessary. The only other main intervention by zoo staff was when a new infant was around two months of age, it was caught along with its mother and was sexed and microchipped (occurred in Zoo E during study). The microchip contains an identification number where the first half of the number is identical to its mother's identification number and the second half characterizes that individual. This information was then added to the studbook for future reference.

Studbooks from 2001 to 2003, along with the reproductive history of all the female macaques involved in this study, were obtained from the European studbook keeper. A record of the reproductive history of male macaques was not obtained, as males are often transferred between zoos to maintain the genetic diversity in the captive population, making it difficult to continuously establish their reproductive potential due to the complexity of the studbook. The studbooks allowed a family tree of each captive group to be constructed (see Appendix 2). Inbreeding coefficients were also obtained using the ARK's system. The ARK's system is an animal record keeping system or database that is used to inventory zoo animals and record specific care information about these animals. Each zoo needs to maintain this system as part of the International Species Information System (ISIS). Thus, inbreeding coefficients of a captive species is the type of information held on this database and this gave an indication on how inbred the British and Irish captive population was. These values were incorporated into the family trees (see Appendix 2).

2.3. Pilot study

A pilot study was carried out at Zoo B for a period of ten full days. During this time, continuous focal animal sampling was carried out to enable the observer to become familiarised with this species. Behavioural categories were defined and an ethogram constructed (see Table 2.3), along with individual identifications of the particular study group.

In order to identify individuals within the study group, descriptive detailed notes were taken which included face shape (whether it was round or thin), the length and shape of the mane (whether it was long and big or short and cropped), whether it was a large or a small individual, whether individuals had dependents etc (see plates 1 and 2). Most groups varied in age and age is related to body size and sex, which made identification easier. Female offspring tended to take on characteristics similar to their mother, thus if the mother had a wide face and large mane, in the majority of cases the daughter also showed these facial characteristics.

a) Individual 14

b) Individual 7

Plate 1 (a and b): Example of differences in face shape used as a method for identification of individual lion-tailed macaques.

The pilot study allowed the appropriate focal animal sampling period and the times of sampling throughout the day to be defined.

Table 2.3. Ethogram

Type of behaviour	Description
Active	
Locomotion (Lo)	Movement of whole body either walking, running, swinging or jumping.
Self play (Plse)	Involves manipulation of objects such as ropes.
Inactive	
Resting (R) including Dorsal huddling (Rdh) and ventral huddling (Rvh)	Sitting or lying down. Sometimes huddling with another. Either dorsal huddling (animals ventral surface in contact with recipients back and huddler with arms around its waist) or ventral huddling (animal facing its partner, with arms wrapped around partner).
Food related	
Feeding (Fe)	Process of manipulating (feeling/playing) and consuming food. Preparation before ingestion of food.
Foraging (Fo)	Process of searching for and handling of food, involving locomotion.
Social	
Allogrooming (Al)	Where one individual grooms another involving the manipulation of fur and removal of foreign bodies.
Aggression (Ag)	Aggressor exposes its teeth with a direct stare at recipient. Lip smacking may occur. Physical contact or chase behaviour may also occur.
Infant related (Suckling/Clinging) (InS/InC)	Interaction between infant and adult (especially mother). Suckling of nipple or clinging to fur.
Mating (Ma)	Adult male examines female's anogenital area manually, sniffs it and then mounts oestrus female and pursues copulation. Thrusting and grunting occurs and female sometimes elicit staccato vocalization.
Mounting (Single/Multiple) (MoS/MoM)	Adult male climbs onto female and does rhythmic pelvic thrusting (copulation), this may or may not result in ejaculation. May be multiple or single mounts.

Social Play (Plso)	Often by infants and juveniles involving behaviours such as chase, wrestling, biting etc
Facial display (Threat/Appeasement/Mixed) (FdT/FdA/FdM)	Threat display where canine teeth are exposed and individual has a fixed stare/Appeasement is a grin (grimace) where lips are slightly parted exposing a small portion of the canines/Can be a mixed facial display between the two types.
Other	
Autogrooming (Au)	Grooming of self, involving the manipulation of fur and removal of foreign bodies.
Lip smack (LpS)	Rapid opening and closing of lips with audible smacking sound.
Sexual inspection (manipulation/masturbation) (Sxman/Sxmas)	Inspection or manipulation of genitals. Possible masturbation by male.
Grunt vocal (GruV)	Adult female grunts when male dismounts.
'Coo' vocal (CV)	Females and juveniles sometimes whine prior to, and during feeding and foraging. Also observed when individuals are pacing round the cage. A contact call.
Squeal vocal (SqV)	Response to a threat or aggression
Cluck vocal (ClV)	Produced by an infant when they are either rejected or restrained by its mother
Staccato vocal (StV)	Produced by female during copulation. Also sometimes emits a stutter vocal, which is a rapid guttural vocal to attract the male.
Growl vocal (GroV)	Aggressive vocal that is directed to the keeper
Hand to eye (H2E)	Individual places either left hand to left eye or right hand to right eye and appears to be focusing on a distant object.
Out of sight (OOS)	Individual not in view
Other	Behaviours that don't fit into named categories

2.4. Experimental procedures

It was found that three sampling periods throughout the day would be used taking into account that the largest captive group in this study was made up of 11 individuals, thus these sampling periods enabled data to be collected within the same time period for each zoo. Each sampling period consisted of a maximum of 2 hours behavioural sampling depending on the number of individuals within the group. These sampling periods were classed as: Morning (0900h to approximately 1100h), Midday (1200h to approximately 1400h) and Afternoon (1500h to approximately 1700h). Fifteen days in total was allocated to each zoo for familiarization with individuals, drawing of enclosure maps and to allow for any problems with the captive group, such as any serious veterinary care that had to occur that would disrupt the behaviour of the macaques. Twelve days of data was collected per zoo giving a total of 60 days of data collection at all five zoos, and a maximum of 360 hours of behavioural data (see Figure 2.1 for timeline of project). 12 days of data was collected to make the results more valid, as several days were averaged instead of using data from one day. The sampling periods above were used in each of the three experimental procedures as listed below and the different sampling techniques used in each experiment are discussed in the relevant chapters.

Chapter 3: *Social structure and spatial relationships*

In comparison with other species little is known about the social system of the lion-tailed macaque and it is often difficult to monitor this species in the wild (see Chapter 1). Due to the species being endangered and wild populations becoming fragmented, an understanding of the general characteristics of lion-tailed macaques and their social system would provide an insight into ways of protecting the fragmented populations in the wild.

Therefore, this study assessed the social structure of captive lion-tailed macaques within all five zoos and described the relationships within the groups. This involved mapping

the positions of individuals within the group at regular intervals and transferring this information to a computer programme that calculated the average separation distance between individuals (full details are given in Chapter 3). From this, relationships between individuals could be related to the average separation distances within the group.

Chapter 4: *Activity budgets*

Comparisons of the activity budgets of groups of lion-tailed macaques enabled the welfare of captive macaques to be assessed. In addition, comparing activity budgets of captive groups with those of wild populations, indicated if specific requirements are being met for this species regarding housing and husbandry routines.

Therefore, this study investigated the activity budgets of the five groups and comparisons were made between zoos. This involved recording the behaviour of individuals during set periods of time, so that full activity budgets for each individual and thus for the group could be constructed. The effect of time of day was also investigated to determine if this influenced the activity budgets of lion-tailed macaques (full details are given in Chapter 4).

Chapter 5: *Environmental influences*

It was expected that activity budgets would vary between individuals and more importantly between zoos, therefore the third study investigated external factors such as visitor numbers and enclosure size to determine how these may influence the activity budgets of lion-tailed macaques. This involved ranking zoos on enclosure size, enclosure complexity, type of feeding regimes and the visitor numbers and thus correlating these ranks with the macaques' behaviour (full details are given in Chapter 5).

2.5. Descriptive and statistical analysis

Where appropriate graphs were produced to summarize results, particularly when making comparisons between zoos (see chapters, 3-5).

Normality tests were performed on all data sets and the appropriate parametric or non-parametric tests were performed, as detailed in each of the experimental chapters (Chapters 3, 4 and 5). In general one-way ANOVA tests were performed on data for both Chapters 3 and 4. Pearsons correlations were also performed in Chapters 3 and 5 and Kruskal Wallis tests were performed in Chapter 4.

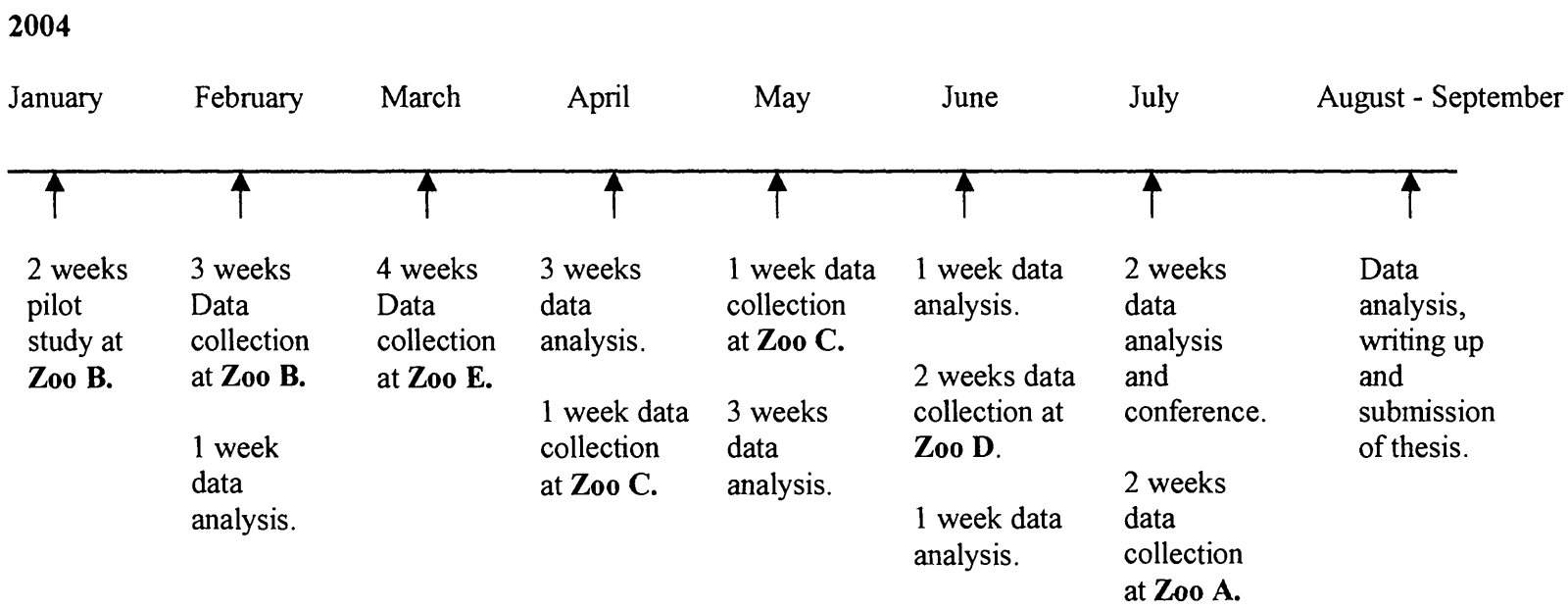


Figure 2.1. A timeline of data collection and analysis during the one year study period.

CHAPTER 3: SOCIAL STRUCTURE AND SPATIAL RELATIONSHIPS

Abstract

Primate social systems have been well documented amongst apes and many Old World and New World monkeys', however, one species that has escaped such investigation is the lion-tailed macaque (*Macaca silenus*). This species is now listed as being endangered on the IUCN red list. Through habitat degradation, the remaining wild populations are occupying forest fragments and thus becoming increasingly isolated. As lion-tailed macaques housed in captivity are restricted to a certain area, it is possible that they could be used as models for management protocols of the wild fragmented populations. The aims of this study were to investigate the social structure and spatial relationships of the British and Irish captive population of lion-tailed macaques and to investigate whether the social structure and space available within enclosures was related to the reproductive success of this species in captivity. The spatial separation distances between individuals were measured using the Animal Tracker® computer software programme. It was found that social structure varied between the five zoos and this was due to group size. Reproductive success and the age at which females reproduced varied within and between groups, possibly due to a lack of novelty for females in choosing mates. Relationships between female lion-tailed macaques, such as whether females were related or not, and thus dominance hierarchy appeared to influence the spatial separation distances between individuals, although not significantly. Enclosure size did not to a significant influence on the spatial separation distances. As this study had a small sample size it is possible that significant results would have been found if more zoos were included in the study. In conclusion, as mentioned above, it is possible that captive populations could be used as models of wild fragmented populations. The findings of this study would suggest that in fragmented populations, smaller groups may affect social structure, the reproductive rate may decrease and the dominance hierarchy may be affected.

3.1. Introduction

Primate social systems have been investigated for many years, with research being undertaken on both Old World and New World primates. Social organization, social structure and mating systems are said to be the main components that influence a primate social system (Kappeler & van Schaik, 2002). Social systems have been well documented in the majority of primates, for example, in chimpanzees (*Pan troglodytes*) (Wittig & Boesch, 2003), Hamadryas baboons (*Papio hamadryas hamadryas*) (Zinner *et al*, 2001) and the majority of macaque species such as the Japanese macaque (*Macaca fuscata*) (Koyama, 2003) and the long-tailed macaque (*Macaca fascicularis*) (Chapais & Gauthier, 2004) to name just a few.

In general, macaque species exhibit a multi-male/multi-female structure and there are four important features that characterize this type of social structure. The first is that a population consists of several adult males, two to three times as many adult females and a number of juvenile offspring. Secondly, within each group a social dominance hierarchy exists, which determines access to certain limited resources such as food and novelty items. Thirdly, new groups are formed by the division of pre-existing ones, usually along matrilineal lines. And finally, male macaques almost always migrate from their natal group before reaching sexual maturity, while females ordinarily remain in their natal group throughout their life (Melnick & Hoelzer, 1996). Dominance hierarchies are considered to be important in terms of the operation of macaque societies. In a typical matrilineal hierarchy, as exhibited by macaques, a mother's rank determines her daughter's rank, thus high ranking females give birth to high ranking daughters (Chapais & Gauthier, 2004). However, with lion-tailed macaques there is little specific information regarding the social structure and organization of this species under natural and captive conditions. This is probably due to problems associated with studying lion-tailed macaques in their natural environment and also due to their small population numbers (see Chapter 1). There are three types of mating systems in primate societies, the first being polygyny where the male maximizes his fitness by mating with many females, the second being monogamy in which each adult mates with only one member of the opposite sex, and thirdly promiscuity, where both males and females mate with more than one

member of the opposite sex. Monogamy occurs particularly in New World primates where the male plays an active role in parental care. For example, marmosets (*Callithrix*) and tamarins (*Leontideus*) usually produce twins and the male carries one of the infants when the mother is not nursing (McFarland, 1999). Macaques are generally a polygynous species with the dominant male mating with several females. However, on the odd occasions sub-ordinate females may mate with a surplus male that sits on the periphery of the group.

Since this species is endangered, it is important to gain an understanding of its behaviour, as many wild populations are now split into small isolated populations due to habitat degradation and consequently are isolated and restricted to a certain area. Therefore, in order to mange the wild population the behaviour and social structure of lion-tailed macaques in general needs to be analysed. This is where captive populations can be useful, as in a sense they mimic what is now occurring in the wild due to the group being restricted to a certain area, limited resources and a decrease in the turnover rate of males, thus possibly influencing the reproductive success of this species. It is thought that lion-tailed macaque groups in captivity, differs from the wild population, thus consequently the social structure would differ between zoos but some groups would mimic those in wild fragmented populations and with other macaque species.

It is well documented that male lion-tailed macaques migrate once reaching adolescence (Ananda Kumar *et al*, 2001). In a captive setting, group structure is controlled and attempts are made to maintain a polygynous situation in lion-tailed macaques groups. Thus, zoos try and retain as many females as possible within the group and move juvenile males once they reach sexual maturity, or before then if they are disrupting the group by showing aggression towards other individuals, in particular towards the dominant male. The dominant male is also often exchanged between zoos to maintain the genetic diversity within the captive population.

It is hypothesised that captive groups with a history of low reproductive success may have had a low rate of male turnover. Knowledge of the male turnover rate in the

captive population would give an indication of how this affects the reproductive success of this species, as there is a suggestion that females are attracted to new males and thus mating is high when a new male has been introduced into the group, however, this novelty appears to decrease over time and thus the rate of mating also decreases (Harvey & Lindburg, 2001). There are however possible welfare implications of changing the social structure of a group in order to increase reproductive success are discussed in terms of the welfare of individuals within the group.

In conclusion, studying the social structure and spatial relationships of lion-tailed macaques might provide clues regarding why this species has a low reproductive success in captivity as well as state the possible consequences for the wild fragmented populations if they become continuously isolated. As the lion-tailed macaque is a matrilineal species, it is thought that closely related individuals may have on average a lower spatial separation distance between them and the dominant female compared with separation distances between unrelated individuals and the dominant female, and that enclosure size may influence these separation distances.

3.1.1. Aims of the study

(i) Social structure

The first aim of study was to see how the social structure of lion-tailed macaques differs across the British and Irish captive population.

(ii) Dominance hierarchy and spatial relationships

The second aim was to see whether the spatial distance between individuals was related to their relationship to the dominant female.

(iii) Reproductive success and mating systems

Finally, the third aim was to see how the social structure and space available within the enclosure relates to the reproductive success of the group and thus establish the mating system of this species.

3.2. Methods

Five zoos (Zoos A-E) were used in this study, as described in the general methodology chapter (see Chapter 2, section 2.1.). Social structure, reproductive success, dominance hierarchies and spatial relationships were assessed using the studbooks (Krebs & Kaumanns, 2003) and 'ARK's system (an animal record keeping system, as detailed in Chapter 2, section 2.2) and this information was used to construct family trees. Spatial separation distances between individuals were calculated using the computer programme, Animal Tracker®.

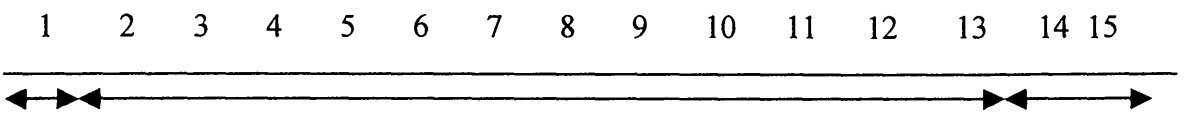
3.2.1. Social structure and reproductive success

In order to assess the social structure and reproductive success of each group, family trees were constructed before arriving at each zoo (see Appendix 2). This was done using information from studbooks and the ARK's system for each zoo. The studbook lists the individuals held at each institution and each individual has its own studbook number. In addition, individual's include details of the studbook identification numbers of both parents. Therefore using this information, relationships such as mother and daughter or sisters could be established and thus family trees could be constructed. The reproductive success and thus potential of each female was calculated by dividing the number of living offspring by the number of births and converting this figure to a percentage. The data for this calculation was found using the 'ARK's system which lists for each female in the captive population, the number of births and the number of surviving offspring. This system also identified the age at which each female gave birth, and this is summarised in Appendix 2. The inbreeding coefficient for each individual was taken from the studbooks and incorporated into the family trees. This coefficient indicates the probability that the two alleles for any gene are identical by descent, resulting in a reduction in fitness of that individual (Kalinowski & Hedrick, 2001).

3.2.2. Dominance hierarchies and spatial relationships

Fifeteen days were spent at each of the zoos (Zoos A – E). The days were split into days for preparation and days for data collection (see Figure 3.1).

Figure 3.1. Timeline for analysing the social structure, including dominance hierarchies and spatial relationships in captive lion-tailed macaques at each zoo.



Day 1	**Days 2 – 13**	**Days 14 & 15**
Scale diagrams of enclosures drawn (see below). Enclosures were graded based on size (see Table 3.1). Observations of group were carried out to familiarise observer with individuals.	Data collection period. Group was scanned every 10 minutes and positions of individuals were recorded on enclosure maps during three sampling periods (see Chapter 2, 2.4).	Extra days in case of any problems incurred during data collection period, such as extensive veterinary treatment of individuals.

Dominance hierarchies

Day 1 was spent drawing a scale diagram of the indoor and outdoor enclosures (see Appendix 3) from maps obtained from the zoo's estates office. This was done using the paint shop programme in Microsoft Office 2000 (see Appendix 3). The overall enclosure was given a grade (1 – 5) based on size (see Table 3.1). For example, if a zoo was ranked one, it meant that the enclosure was small in relation to the number

of individuals within the group, as size was based on space allowance per individual. This was calculated by dividing the number of individuals within the group by the total area of enclosure (both indoor and outdoor enclosures).

Table 3.1. Descriptions of grades allocated to zoos based on size of enclosure.

ENCLOSURE SIZE GRADE	ZOO	DESCRIPTION OF ZOO
1	B	Overall small enclosure, limited space for the number of individuals held within the group.
2	D	Medium sized enclosure ranging between grades 1 – 5.
3	E	
4	C	
5	A	Overall very large enclosure, large space per individual.

With the aid of the family trees, information on relationships within the group and the dominance hierarchy were identified. This was achieved by observing the individuals in their home enclosures, and recording interactions within the group, particularly during feeding and allogrooming, where this behaviour was mainly carried out between related individuals. Dominant individuals were defined as those individuals that were the winners of aggressive encounters with other members of the social group and thus displaced the subordinate individuals from food by chasing these individuals away from the food source or eliciting aggression and then mounting that individual to confirm their dominance. Close attention was paid towards the adult females, as the ranking of the female is known to affect the ranking of her offspring (Chapais & Gauthier, 2004). By determining the relationships between individuals it was possible to formulate the dominance hierarchy. Generally, dominance hierarchy is age related (McFarland, 1999), so in the case of sisters, the older sister tends to be dominant. Males were ranked separately, as in most cases there was a dominant male who was observed to lead the group and usually one juvenile male who is normally considered to be at the bottom of the hierarchy until maturity, when juveniles disperse in the natural environment.

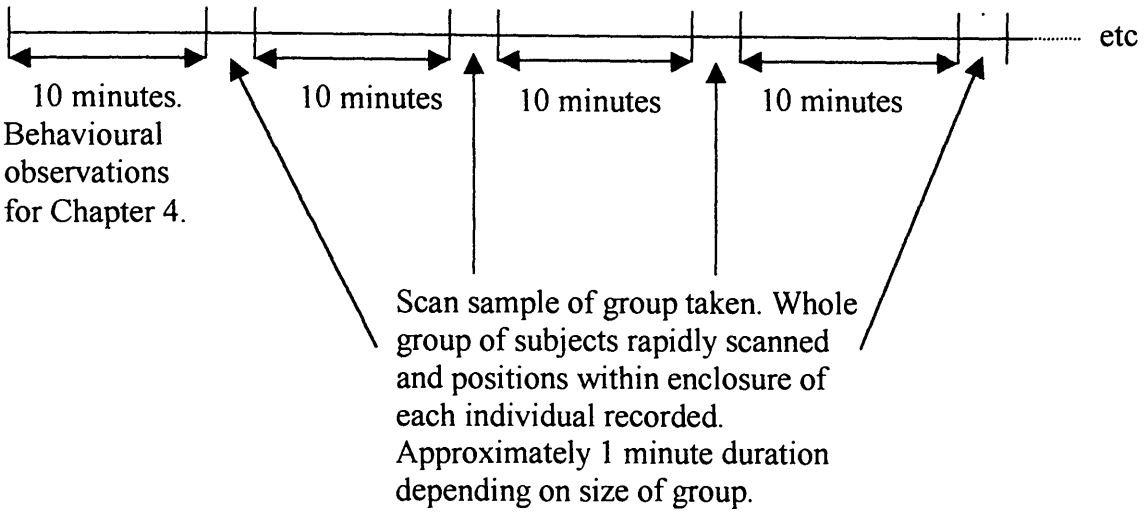
(i) On Days 2 - 13, behavioural observations were made of the whole group in order to determine

a) If the average spatial separation distances between individuals was related to the relationships within the group.
b) If the size of the enclosure influenced the average spatial separation distances between individuals within the group.
c) If the average spatial separation distances varied between zoos.

Observations were carried out at each zoo by the same observer.

Day 2 was the first day of data collection. Every 10 minutes, a scan sample was taken where the whole group of subjects was rapidly scanned and the positions of each individual within the group were recorded on the enclosure maps. The number of scans taken depended on the number of individuals within the group as scan samples were taken at the same time as behavioural observations for Chapter 4. Thus, the number of scans per group was equal to the number of individuals plus one (n + 1). For example, as zoo B had five individuals this gave six spatial scans (i.e. six recordings of individual positions) in total for the morning sampling period. Thus, after the three sampling periods 18 scans had been obtained for that particular day. This procedure was then repeated for another 11 consecutive days, giving 216 scans in total for Zoo B.

Figure 3.2. Timeline of data collection for spatial separation distances between captive individual lion-tailed macaques. During each of the 10 minute samples, behavioural observations were recorded for Chapter 4.



The data collected on the spatial maps were then transferred to a computer program called Animal Tracker®. In Animal Tracker® the enclosure was drawn to scale and then the position of each individual for each scan was placed onto this map. The program then calculated the average distance between all individuals for each scan, formed averages for each day and then constructed tables for each day to summarise these averages. This procedure was repeated for each zoo.

Two of the groups contained dependents (i.e. offspring that had not been weaned), thus altering the group number and composition. However, depending on when the birth was, many infants remained solely attached to their mothers, thus the mother and infant were included as one focal observation, however, interactions between mother and infant were recorded.

3.2.3 Descriptive and statistical analysis

3.2.3.1 Description of spatial data

Using the Animal Tracker® computer program, the distances between individuals within the group were calculated for each scan. This was then averaged for each day. As the 12 days were pseudoreplicates (i.e. repeats of the same observations) the distance data were once again averaged over the 12 days. Tables were then constructed (see Appendix 4) giving a single average separation distance between individuals of the group. This in turn was used to illustrate the social structure and spatial relationships of the group as a whole and enabled visual comparisons to be made between groups. To summarize these relationships, spatial maps were drawn for each zoo (see Figure 3.5). These spatial maps were constructed using the paint shop programme in Microsoft Office 2000, where each line drawn from the dominant female in the centre of the diagram represented to scale the average distance that a particular individual was from the dominant female. Included in these spatial maps were the ranks of each individual in relation to the dominance hierarchy for the group. For example '3 Individual 25 (F)' meant that this was individual 25, it was a female and was ranked third in the dominance hierarchy. The dominant male, however, was not ranked as this species, as already stated, is a matrilineal species, thus the male normally sits on the periphery of the group, and these maps were summarising the relationships in relation to the dominant female.

3.2.3.2 Statistical analysis of spatial data

The average distances between individuals, were tested for normality using one-sample Kolmogorov-Smirnov test in SPSS (version 12.0).

Relationships between the dominant female and other individuals were categorised as: sister, brother, mother, daughter, son, niece, or unrelated. If the data were found to be normally distributed, one-way ANOVA tests were performed using Minitab statistical software (version 12.0) to investigate differences between categories in the

average separation distance between the dominant female and other individuals within the group. One-way ANOVA was also carried out to investigate differences between the dominant male and each of the top three ranking females.

Two-tailed Pearsons correlations were also performed using SPSS (version 12.0) to assess whether the distances maintained within the group were strongly influenced by enclosure size. This was done by correlating individual distance data with the space allowance per individual. The space allowance per individual was calculated by dividing the number of individuals within the group by the total area of the enclosure (both indoor and outdoor exhibits).

3.3.1. Social structure and reproductive success

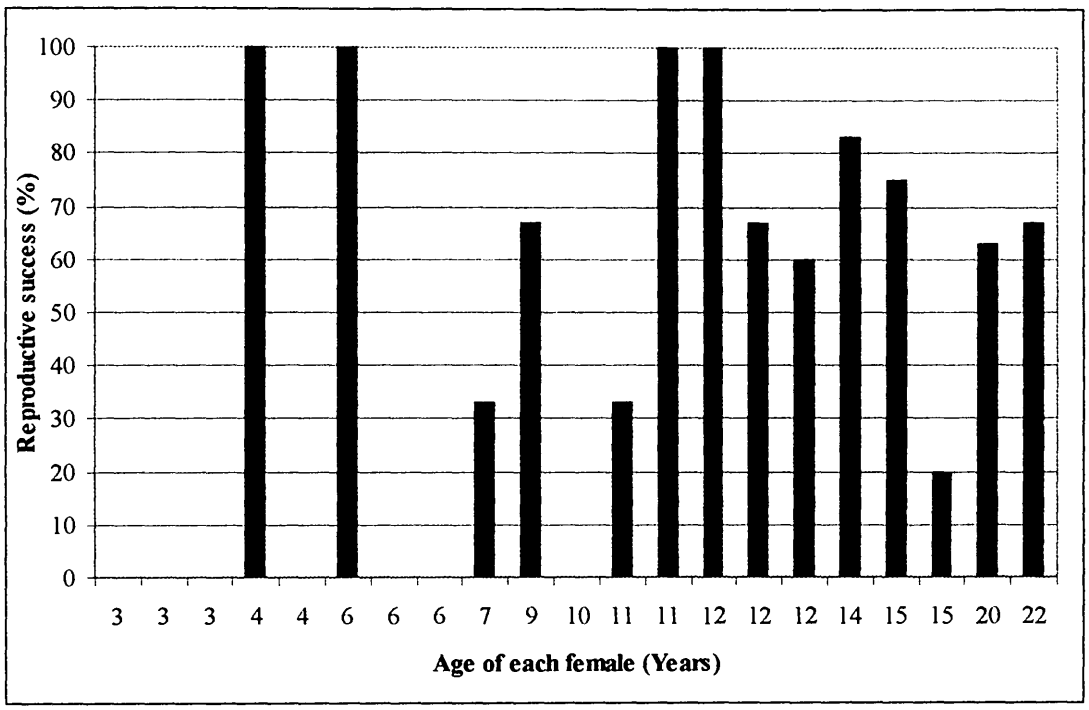
The family trees (see Appendix 2) confirmed which groups had shown the most breeding success. It was found that Zoos A, C and E had the largest groups and thus possibly the highest reproductive success. It is important, however, to take into account that despite the fact that groups with older individuals would most likely be successful, these individuals could have a high number of births during their lifespan but also have a high percentage of these births resulting in infant mortality. Thus, individually, reproductive success of females varied within and between groups (See Table 3.2. and Figure 3.3.).

Table 3.2. The reproductive success to date of all females aged four years and over (Zoos A to E).

Zoo	Individual number	Age (Years)	Reproductive success to date (%) (Number living/Number born)
A	1	22	67 (4/6)
A	7	15	75 (3/4)
A	8	6	0
A	2	7	33 (1/3)
A	4	12	100 (2/2)
A	5	6	0
B	13	15	20 (1/5)
B	9	12	67 (2/3)
B	12	3	0
C	19	11	33 (2/6)
C	22	9	67 (2/3)
C	14	4	0
C	21	3	0
D	26	10	0
D	25	14	83 (5/6)
E	34	20	63 (5/8)
E	31	12	60 (3/5)
E	32	3	0
E	27	11	100 (1/1)
E	35	4	100 (1/1)
E	29	6	100 (1/1)

Some females had a reproductive success of 0 as they had not reached sexual maturity with one exception, which was individual 26 at Zoo D, who had not given birth from an early age and subsequently had had her uterus removed for medical reasons. Only two groups (Zoos C and D) had started to show inbreeding coefficients (see Appendix 2).

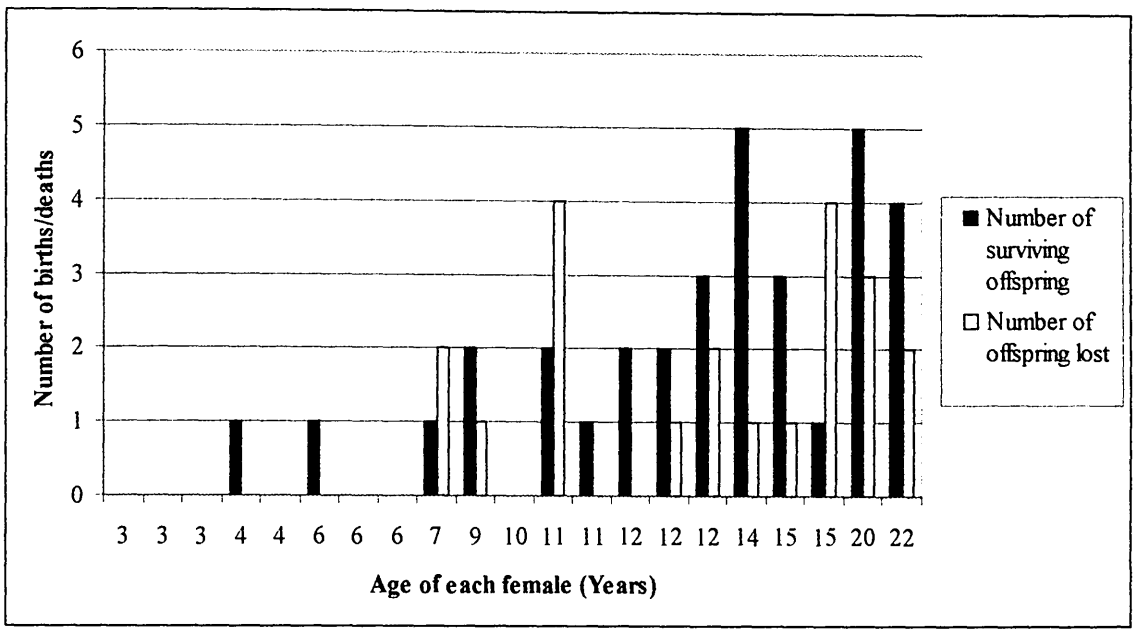
Figure 3.3: The reproductive success of female lion-tailed macaques aged four years and over in the study population.



The number of offspring that have died through stillbirth or within the first few hours of life varies between individuals (see Figure 3.4).

From the information gained from the studbook (Krebs & Kaumanns, 2004), it was also observed that infants that had died either from stillbirth or during the first few days of life showed a sex bias. It was found that 70% of deaths were males, 21% were females and 8% were of sex that was unrecorded.

Figure 3.4. The number of surviving offspring and the number of offspring that have died in relation to the age of female captive lion-tailed macaques in the study population.



3.3.2. Spatial relationships and dominance hierarchies

From the spatial maps (see Figure 3.5. a, b, c, d, and e) it was seen that Zoos B and C showed the smallest average separation distances between individuals and the dominant female. Zoo C in particular showed the smallest separation distances and this was partly due to the fact that the majority of the individuals were related to each other. This is even more evident when comparing Zoos C with A, D and E where these groups contained unrelated individuals. At Zoo A there were two individuals, a mother and daughter (individuals seven and eight) who were unrelated to the dominant female and hence her offspring, thus they tended to show the greatest separation distances in comparison with other members of the group. At Zoo D the two females were unrelated and thus have a wide separation distance, however, they are the only two females within the group so do spend some time in closer proximity such as during grooming regimes. In Zoo E, the females were subdivided into a dominant and a subordinate group. Thus, the subordinate group (females ranked 6 – 9), which was led by individual 31, had a larger separation distance in relation to the

dominant female and her offspring (females ranked 1 – 5). In the three zoos that had a dominant male, the dominant male tended to be closer in proximity to the dominant female in comparison with unrelated females. For example, in Figure 3.5 (e), the dominant male was much closer in proximity to the dominant female (individual 34) in comparison with the proximity of the subordinate group (females ranked 6 - 9) to the dominant female.

Figure 3.5. a, b, c, d, and e: Spatial maps for all five zoos (Zoos A – E) including key for spatial maps.

Key:

M = Male
F = Female

1 = most dominant
10 = lowest ranked

Relationship to dominant female:

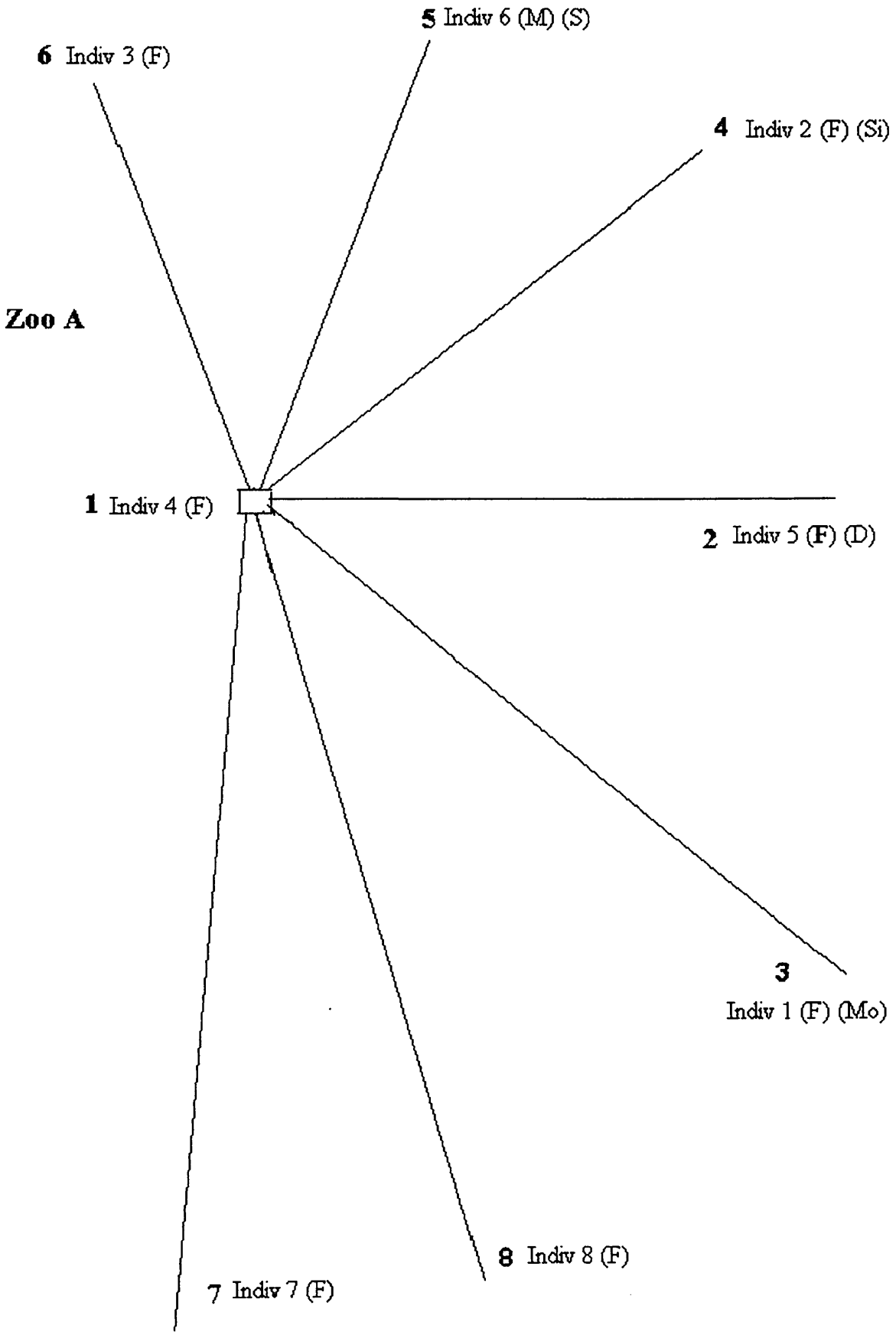
D = Daughter
S = Son
Si = Sister
B = Brother
Mo = Mother
Ni = Niece
Dom M = Dominant Male

Scale:

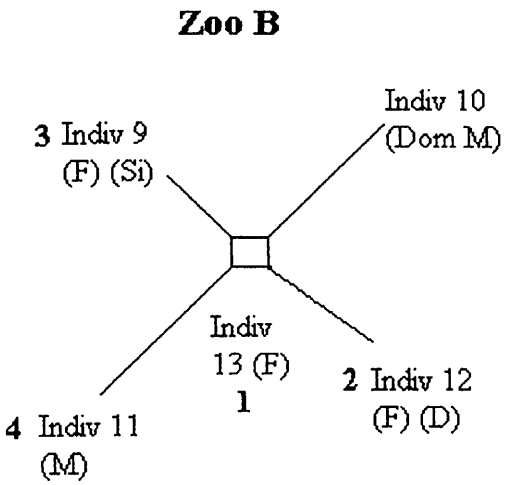
____ 1 cm = 1 m

*The shortest lines indicate close relationships, however the angles between the lines do not represent anything.

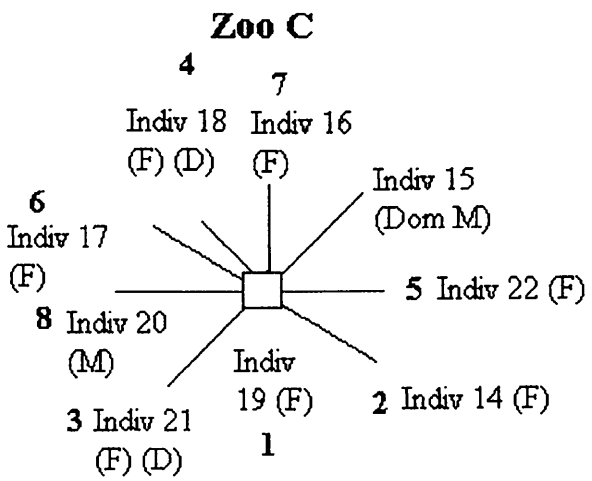
a) Zoo A


5 Indiv 6 (M) (S)
6 Indiv 3 (F)
4 Indiv 2 (F) (Si)
Zoo A
1 Indiv 4 (F)
2 Indiv 5 (F) (D)
3
Indiv 1 (F) (Mo)
8 Indiv 8 (F)
7 Indiv 7 (F)

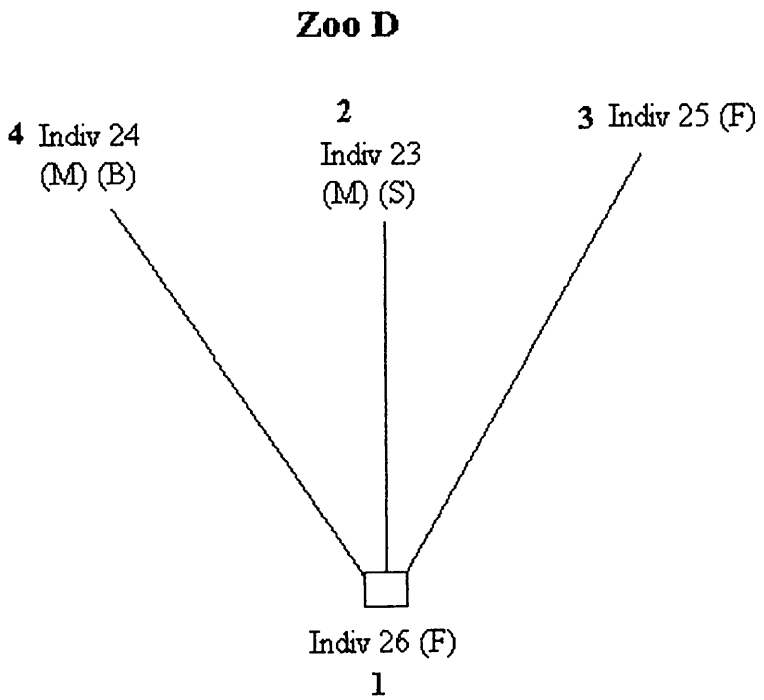
b) Zoo B



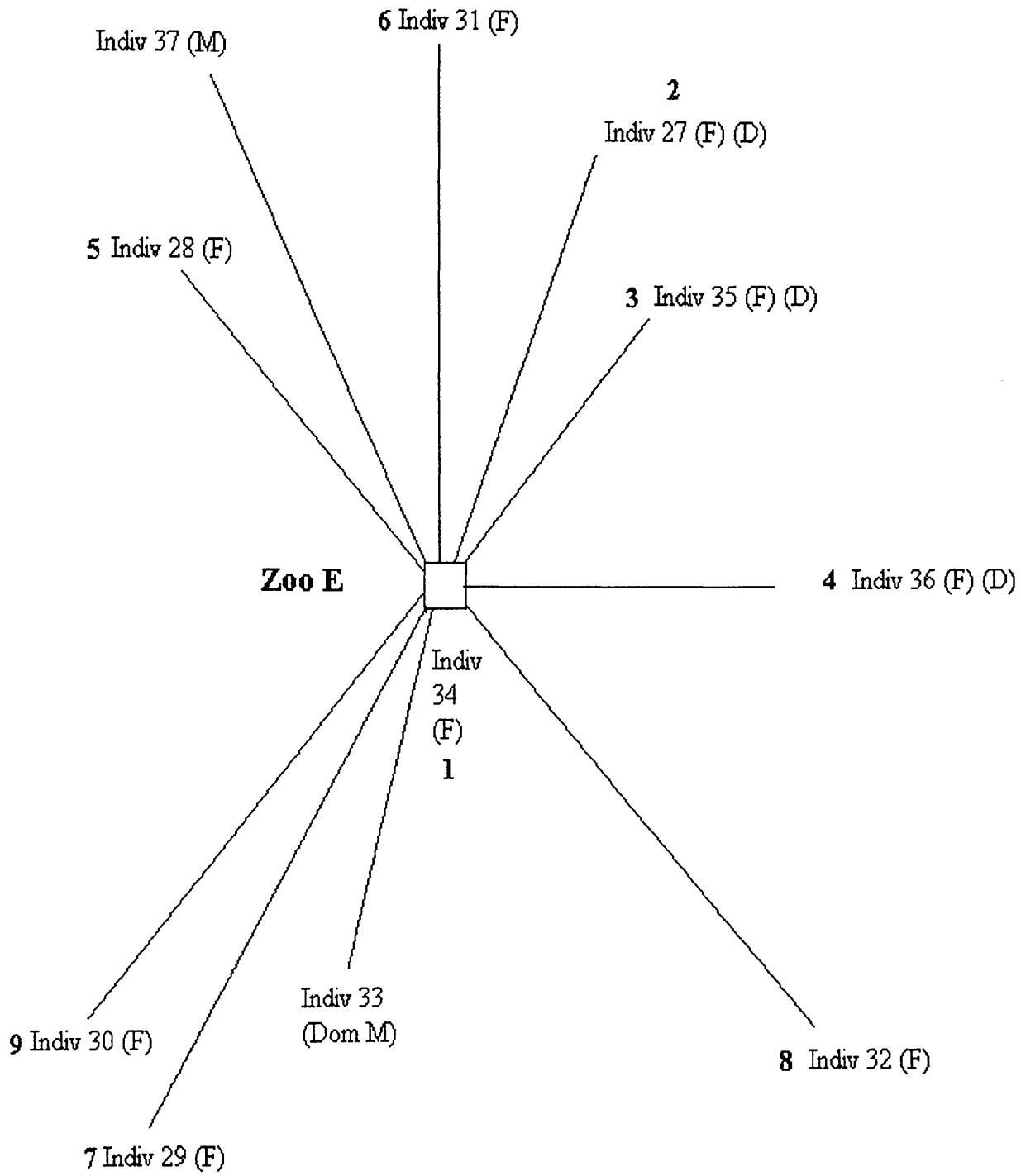
c) Zoo C



d) Zoo D



e) Zoo E


6 Indiv 31 (F)
Indiv 37 (M)
2
Indiv 27 (F) (D)
5 Indiv 28 (F)
3 Indiv 35 (F) (D)
Zoo E
4 Indiv 36 (F) (D)
Indiv
34
(F)
1
Indiv 33
(Dom M)
9 Indiv 30 (F)
8 Indiv 32 (F)
7 Indiv 29 (F)

When comparing the distance between dominant female and other individuals based on their relationships to the dominant female (i.e. sister, brother, mother, daughter, son, niece, or unrelated) no significant differences were found. Also when comparing the average separation distance between the dominant male and each of the top three high ranked females no significant differences were found. Statistically, the relationships within the groups therefore appear to have no effect on the average distances between individuals.

Although Zoo C showed small average separation distances in comparison with the other four zoos it had the second largest enclosure based on space allowance per individual (see 3.2 Methods, Table 3.1). However, when assessing if distances maintained within the group was strongly influenced by enclosure size it was found to be non-significant.

3.4. Discussion

3.4.1. Social structure

In this study it has been found that social structure differs amongst the British and Irish captive population of lion-tailed macaques and is likely to be affected by group size. The largest group consisted of 11 individuals with the smallest group being made up of only four individuals. In comparison with wild populations both group sizes are small. For example, in Silent Valley National Park, Kerala, India, 14 troops were identified with the smallest troop consisting of nine individuals and the largest group consisting of 36 individuals (Ramachandran & Joseph, 2000). All groups had at least one adult male, possibly a sub adult male, more than four adult females and at least four immature individuals.

When comparing the social structure of the wild population with the study population, it was obvious that there were differences. For example, Zoos A and D lacked a dominant male (see Appendix 1), and Zoo D also had two juvenile males of similar ages (individuals 23 and 24). However, when collecting data from Zoo D, it was found that one of the juvenile males (individual 23) had been castrated to avoid inbreeding through mating with his mother (individual 25). At present, individual 23 is dominant over individual 24, however, it is hoped that individual 24 will become the dominant male, as he is unrelated to individual 25 and it would mean that a replacement dominant male for this group. In regards to Zoo A, an adult male has been found from another zoo to be introduced into the group and thus take the position as dominant male. There is currently only a one year old juvenile male (individual 6) present in the group and thus no males for this incoming male to compete with. There is a risk of infanticide, however, with the introduction this new male (Kaumanns, pers. com). The juvenile male is only one year old and there is also a seven month old infant (individual 3) within the group, which are both at risk. Infanticide by males has been hypothesized to be a naturally selective behavioural strategy that increases the infanticidal male's reproductive success, and this has been documented in a number of species such as in chimpanzees (*Pan troglodytes*) and in

wild patas monkeys (*Erythrocebus patas*) (Enstam *et al*, 2002). Therefore, the timing of when this male is introduced into the group is crucial, particularly as it is unknown whether any other females within the group are pregnant by the previous male.

Zoos C and D have started to show inbreeding coefficients, indicating homozygosity in alleles and thus a decrease in the fitness of individuals. Although these are of very small proportions, at present it does indicate that future plans need to be made regarding the exchange of the dominant male, so that new genes can be added into the groups. However, once again, the timing of this is crucial to reduce the risk of infanticides. These factors, such the risk of infanticide by introducing males, will influence the social structure of the group and consequently will affect the reproductive success of the captive population.

3.4.2. Reproductive success

The number of individuals within groups of the study population are low, however, the European captive population as a whole has doubled since 1990 (Kaumanns *et al*, 2000). An important factor that influenced the size of these groups was the reproductive success of the group in relation to the group's reproductive potential. In the study population the females' reproductive success varied considerably (see Figure 3.3.). Reproductive success as predicted but this fluctuated dramatically between individuals and between zoos. This seemed to relate to what has been observed when looking at the demography of the European population as a whole. Problems that are developing within the European captive population include a biased age/sex composition towards adults and in particular towards individuals which are greater than 15 years old (Kaumanns *et al*, 2000). There were a larger number of females aged between four and fifteen years of age, which should be able to reproduce. However, it is now evident from the numbers of individuals in the younger age classes that they reproduce less frequently and less successfully (Kaumanns *et al*, 2000). From Table 3.2 it can be seen that individuals 8, 5, 14, 21, 26 and 32 had a reproductive success of 0%. All these individuals were under six years old with the exception of individual 26 who were ten years old, but due to

medical complications had had her uterus removed and thus is unable to conceive. In the wild, females are said to reach sexual maturity at the age of six years (Kumar, 1995b), however, in captivity females have been found to give birth as early as three years of age (individuals 9, 19, 25, 31 and 34), but the majority of these births have resulted in infant mortality where the infant has been stillborn. This was possibly due to underdevelopment of the infant in the womb and may correlate with the age of the female, although this is only speculative.

A consequence of this unbalance in reproductive output across all age groups, and the fact that numerous founder animals are underrepresented in the gene pool, is that the captive population is at risk of losing its genetic variability as well as the ability to self-sustain in the future (Heistermann *et al*, 2000). Therefore, possible causes of low reproductive success needs to be investigated and management plans formulated.

Previous research has looked at the ovarian function of lion-tailed macaques through the measurement of faecal steroid metabolites (Heistermann *et al*, 2000). It was found that irregularities occurred in the ovarian cycle of these macaques, with some individuals showing an extended follicular phase of up to 70 days, with the normal phase being 31 days in length, thus resulting in infertility. However, these findings were restricted to older study animals (>20 years of age). Similar age effects have been demonstrated for rhesus monkeys and chimpanzees (Heistermann *et al*, 2000). Data on female fertility rates in the North American captive population indicated that female fertility showed a substantial and continuous decline from age 11 onwards, with very low fertility rates being recorded for animals aged 20 years or older (Heistermann *et al*, 2000).

When assessing the reproductive success of females in relation to age, it appears to correlate with that of the American captive population. The number of births were low as there were only 21 females within this study population and out of these, fourteen have reproduced during their lifetime to date (i.e. 67%). Peaks in the number of successful births, however, were by individuals aged between four and six years of age and 11 and 15 years of age. At present eight females are over the age of

twelve, but only two are still reproducing. This is possibly due to the fact that lion-tailed macaques tend to have long inter-birth intervals (Kumar, 1995b). This figure is likely to have improved in the last year as the latest studbook is being updated. Although the current study only represents breeding data from 21 females in captivity, it does give a good indication of individuals' slow and unsuccessful breeding history to date.

A problem with the reproductive rate could be due to factors other than the fertility of females. One factor that seems quite viable is that females who have been paired with a dominant male for a long period of time are less motivated to mate with this male due to the novelty effect (Harvey & Lindburg, 2001). In the wild, surplus males compete with the dominant male for his position within the group. Evidence for this theory comes from the fact that males disperse from their own troop to avoid inbreeding and because they are likely to obtain a higher dominance rank by emigrating to another group (Ananda Kumar *et al*, 2000). It was found that the proximity to and grooming of, a migratory male was higher than that of the resident male. In addition females made most of their sexual presentations towards the migratory male (Ananda Kumar *et al*, 2000). This implies that females will actively show preference towards a migratory (novel) male and thus there is a higher rate of mating when a new male has joined a group. In captivity, it is hard to mimic the wild population in relation to male migration. It has been found that there is a significant decline in the duration of the tumescent phase (swelling phase) over a four-year period and coincidentally, a lowered rate of copulation by the highest ranked male. This would suggest that the absence of turnover in the adult/sub adult male population i.e. reduction of novelty for females in choosing mates, in some way reduced the investment in advertising in a confined (captive) colony. Consequently, the copulation rate might decrease, as males are not encouraged to copulate due to the lack of advertisement by the female (Harvey & Lindburg, 2001). This provides a valid explanation regarding the low reproductive success in the captive British and Irish population and the obvious answer is to frequently exchange males between institutions. However, the introduction of a new male into a group can also result in infanticides. Problems with aggression may also occur between the incoming male

and other individuals within the group, particularly juvenile males. As it is difficult for individuals to escape, the welfare of some individuals may be a cause of concern.

3.4.3 Spatial relationships

It is generally assumed that female primates derive, on average, greater benefits remaining in their natal area than dispersing, and that males benefit more from dispersing because of the nature of the retrospective benefits in relation to the sex-specific determinants of reproductive success (Kappeler *et al*, 2002). Thus, female dispersal is uncommon among female-bonded primate societies, even though there may be a considerable incentive to do so, for example, to avoid potential infanticide by incoming males. Predation risk and the advantages of sharing the costs of group living, such as resource and infanticide defence, with close kin, are assumed to be causal in limiting female dispersal (Payne *et al*, 2003). The lion-tailed macaque certainly conforms to being a female bonded species and in the wild, females tend to be related, however, in captivity, groups can consist of related and unrelated females. As seen in Figure 3.5, females that are related to the dominant female tend to stay in closer proximity to her.

With regards to the average spatial separation distances, it would be expected that there would be a significant difference in the distance between the dominant male and the dominant female compared with the dominant male and other females within the group. However, in this study no significant differences were found. It may also be expected that males that have been in the group for a number of years would have an overall larger separation distance from the dominant female, compared to those males who are newer to the group and thus still establishing relationships with the females. Indeed, in the wild it was observed that a migratory male was in closer proximity to the females compared with the resident male, both when alone within the group and when the resident male was present (Ananda Kumar *et al*, 2001). In the present study population (see Appendices 1 and 4) the male in Zoo B (individual 10) had been with the group for thirteen years, but only had a separation distance of 2.37 metres from the dominant female, whereas the male in Zoo C (individual 15)

had a distance of 1.63 metres and he had been in the group for six years. In contrast, the male at Zoo E (individual 33) had only been in the group for four years but had an average separation distance from the dominant female of 5.60 metres. It would be expected that the size of enclosure would influence these separation distances, with the highest separation distances between individuals being present in larger enclosures. The distance between the dominant female and males in relation to enclosure size was not analysed. However, overall the distance between the dominant female and all other individuals were not influenced by enclosure size.

In conclusion, the relationships between female captive lion-tailed macaques, such as whether individuals were related to each other or not, appeared to influence the spatial separation distances between them, although not significantly. There was no correlation between the time that a dominant male had been present in the group and his spatial proximity to other individuals of the group. Enclosure size was also found not to significantly influence the spatial separation distances, however, the sample size was small and if more zoos had been included in this study a significant result may have been produced.

3.4.4. Dominance hierarchies

The dominance hierarchy within the group is one of the main factors that influences spatial relationships between individuals. It can be expected that in female-bonded species such as the lion-tailed macaque, between group competition will occur between females over food resources. Females are expected to be hostile towards females in other groups, because their reproductive success is potentially reduced by between group competition for mates (Zinner *et al*, 2001). In most captive populations, there is no between group competition. This means that within group competition may occur over food resources and thus the dominance hierarchy is likely to become the major influencing factor regarding access to food. In this current study, it was observed that rank was clearly seen during feeding time. Unrelated, i.e. individuals not related to the dominant female and thus her offspring, or lower ranked individuals, appeared to sit on the periphery of the group and wait until the

dominant members had collected their food. The same has been reported in chimpanzees, where winning contests over food was related to both age and dominance rank (Wittig & Boesch, 2003).

In Japanese macaques (*Macaca fuscata*), it was found that high ranked females formed close or clustered hierarchies, whereas low-ranking females had more dispersed hierarchies (Koyama, 2003). Indeed high ranking females in the captive study population, tended to have lower separation distances from other high ranking females within the group compared with low ranking females and other members of the group. A good example of this was in Zoo A (see Appendix 4), where individual four who was a high ranking female had on average a separation distance of 10 metres from other individuals, where as individual seven who was a low ranked unrelated female had an average separation distance of 16 metres. When investigating the social structure of Japanese macaques, it was concluded that the levels of clustering within the hierarchy appeared to reflect the social cohesion of the group in terms of grooming and coalition forming (Koyama, 2003). In lion-tailed macaques this does appear to be true for some captive groups but not others. For example, Zoo C holds a group made up of a number of related individuals and as may be expected, their spatial separation distances are quite small, however, Zoo E also holds a group of related individuals with only two members that are unrelated but the separation distances are much greater. These differences in separation distances between females were found to be not significant. Once again enclosure size is likely to influence these results, but also the relationship between the dominant female and the oldest unrelated female would have an effect on the separation distance. In Zoo C the dominant female (individual 19) was found to have a close relationship with the oldest unrelated female (individual 22) and they were both transferred to the zoo at approximately the same time, with the dominant male joining them a couple of months later. However at Zoo D, the dominant female (individual 26) appeared not to associate with the unrelated female (individual 25), even though the dominant female was born five years after the arrival of the unrelated individual. It has been discovered that an unusual kinship structure has formed in captive long-tailed macaques (*Macaca fascicularis*), in which juveniles

have been found to outrank their own mothers, and/or several higher-born females and their offspring. In this case, a suggestion was made that juveniles were able to benefit from bridging alliances with higher-ranking individuals and thus the rank-order became unstable (Chapais & Gauthier, 2004). This may explain what was observed in the current study. However, since no previous data has been collected regarding spatial relationships of this species, this can only remain as a hypothesis.

3.5. Conclusion

Thus, it appears that the social structure of captive lion-tailed macaque groups varies and group sizes are much smaller compared to wild populations. This is mainly due to the lack of available facilities to house large groups of captive macaques and also due to the reproductive problems that appear to be facing the captive population, such as low fertility rates and a lack of novelty for females regarding males. The reproductive rate may also be influenced by other environmental factors such as the effects of enclosure size, enclosure complexity, visitor influences and feeding regimes and this will be discussed in Chapter 6.

The degree of relatedness between females appeared to influence the spatial separation distances between individuals, as did the size of enclosure, and although these differences were found not to be significant, the result may have been different if more groups were compared.

As with many primate species, dominance hierarchy is an important feature in a lion-tailed macaque society and as stated above, it may be influenced by grooming and coalition forming. It would be expected that the rate of grooming would be highest in groups where individuals have shown short separation distances and this will be assessed along with other behaviours that make up the activity budget of these macaques in Chapter 4.

Overall, captive lion-tailed macaques may give an indication of what will occur regarding the wild fragmented populations, as in a sense these wild populations will

be restricted to a certain area, as occurs in zoos. Smaller groups in the wild would therefore be likely to influence the social structure and spatial relationships of the group. The reproductive rate may decrease and the dominance hierarchy may also be affected.

CHAPTER 4: ACTIVITY BUDGETS

Abstract

In the wild, the lion-tailed macaque (*Macaca silenus*) is becoming increasingly isolated and therefore restricted due to habitat fragmentation. Studies of the captive population could give a good indication regarding the responses of lion-tailed macaques to restricted habitat and resources. Thus, the aims of this study were to investigate the behavioural repertoire exhibited by captive lion-tailed macaques in different captive groups and to relate the findings of this study to possible management plans for wild groups confined to forest fragments. Activity budgets of lion-tailed macaques were assessed from over 360 hours of observational data obtained from five captive groups. Data were used to determine the mean percentage of state behaviours and the frequency of event behaviours performed during three sampling periods, morning (09:00h – 11:00h), midday (12:00h – 14:00h) and afternoon (15:00h – 17:00h). The effects of time of day, on the macaques' activity budget, and differences between adult and juvenile macaques were also assessed. Results showed that the mean time spent on autogrooming and foraging behaviours significantly differed between zoos, and the frequency of behavioural events varied between zoos across all three sampling periods. It was found that adult lion-tailed macaques showed greater rates of allogrooming and resting, but spent less time involved in social interactions such as play when compared with juvenile behaviour. The effect of time of day was found to significantly influence feeding behaviour with feeding being highest in the afternoon. In general, the activity budgets of the captive study population were similar to the activity budgets of wild fragmented populations thus, it is possible that captive populations could be used as models for wild fragmented populations, but more groups need to be assessed and compared in order to make it a viable comparison.

4.1. Introduction

Field studies that related behaviour patterns to the social and ecological conditions in which they normally occurred led to the development of a subject termed 'behavioural ecology' (Martin & Bateson, 2001). There are three main components to an animal's behavioural ecology. Firstly, natural selection will favour individuals who adopt life history strategies that maximize their gene contribution to future generations. Secondly, adult survival and reproductive effort depends on ecology, the physical environment an individual lives in, its competitors, food, resources, and so on. Thirdly, because an individual's success at surviving and reproducing depends critically on its behaviour, selection will tend to develop animals as efficient foragers, efficient predator avoiders, efficient copulators, efficient parents, and so on (Krebs & Davies, 1993).

4.1.1. Describing behaviour

Behaviour can be described in a number of ways, but the simplest distinction is between describing behaviour in terms of its structure or consequences. The structure is the appearance, physical form or temporal patterning of the behaviour and includes the subject's posture and movements, for example "the monkey was being inactive". The consequences are the effect of the subject's behaviour on the environment, on other individuals or on itself, for example "the monkey was resting" (Martin & Bateson, 2001). Behaviours can be categorized according to the situation that they are exhibited in. For example, behaviours exhibited by one individual that involve another individual within the group, would be classed as social behaviours, such as grooming or playing. Behaviours can be food related behaviours such as feeding and foraging or active behaviours, which involve the animal physically moving and so on. Physical barriers such as when a species is in captivity or if a species occupies a fragmented habitat could influence these behaviours. Thus, often when characterizing a species, an ethogram is constructed. This is a catalogue of accurate descriptions of the discrete, species-typical behaviour patterns that form the basic behavioural repertoire of that species (Martin & Bateson, 2001). The pattern in

which the behaviours are performed over a period of time is termed the activity budget for that species and it is considered an adaptation to environmental influences. Consequently, the activity pattern of a species is an important basis for understanding behaviour (Beltran & Delibes, 1994). Studies of free ranging animals are often hampered by the difficulty of direct observation of the subjects, such as difficulty in tracking them or dangers from other species in the area such as elephants, thus behavioural studies in a captive setting can be an important element to successful captive management of a species and of wild subjects (Weller & Bennett, 2001).

The lion-tailed macaque is one such species that at present in the wild is becoming increasingly restricted and consequently isolated due to habitat fragmentation. Therefore, in order for this species to survive it is important to understand its behaviour in varying confined habitats. Using the captive population could give a good indication regarding the responses of lion-tailed macaques to varying habitat and resources.

4.1.2. The relevance of studying lion-tailed macaque behaviour

There are many problems associated with studying lion-tailed macaques in their natural environment (see Chapter 1) and due to this species becoming so endangered it is important to understand this primates' behaviour. This indicates its behavioural repertoire, habitat use and thus requirements, reproductive biology and so on. The successful functioning of any primate society emerges partly from the interactions between the individuals of the group and their environment, and partly from the social relationships between the different individuals that comprise the society (Dunbar, 1988).

The social dynamics of a lion-tailed macaque group obviously influences its survival (as discussed in Chapter 3), however, how primate groups apportion their time can provide clues to the species' ability to survive under several ecological constraints (see Chapter 1) (Menon & Poirier, 1996).

4.1.3. Aims of the study

a) Investigate the behavioural repertoire exhibited by captive lion-tailed macaques and compare between different captive groups.
b) Relate the behavioural repertoire exhibited, to the groups' social structure and enclosure design.
c) Relate the findings of this study to possible management plans for wild groups confined to forest fragments, using captive groups as a model.

Knowledge of captive lion-tailed macaque behaviour could indicate possible management plans for the wild population and thus state the implications this has for the long-term conservation of this species.

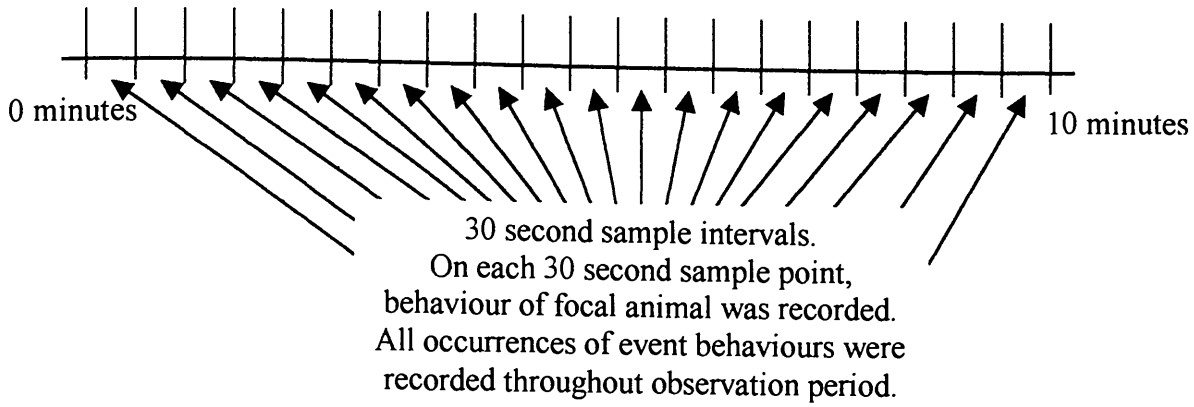
4.2. Methods

4.2.1. Defining behaviours

In order to determine behavioural categories, *ad libitum* observation sampling was carried out where no systematic constraints were placed on what was recorded. This is a useful method of sampling during preliminary observations, however, it is not recommended as the main sampling method as observations can be biased towards those behaviour patterns and individuals which happen to be most conspicuous (Martin & Bateson, 2001).

Once an ethogram had been formed (see general methods, Chapter 2, Table 2.3) behaviours were split into two categories 'states' and 'events'. States are behaviour patterns of relatively long durations such as locomotion, foraging or resting. Events however are behaviour patterns of frequencies, of relatively short duration, such as vocalizations (Martin & Bateson, 2001). At each zoo instantaneous focal animal sampling was used to observe state behaviours within the group and thus enable activity budgets to be constructed. One individual or dyad was observed for an observation period of 10 minutes divided into short sample intervals of 30 seconds (timed using a stopwatch). This meant that the behaviour that the individual was performing at each 30-second sample point was recorded giving 21 sample points of behaviour per individual per sampling period thus giving 63 sample points of behaviour per day. In addition all occurrences of event behaviours were recorded throughout the 10 minute observation period, to give the frequency of events per 10 minute observation period (Martin & Bateson, 2001). As already stated in Chapter 2, three sampling periods were used, thus as each focal animal was observed for 10 minutes per sampling period this gave 30 minutes of behavioural data per focal animal per day (see Figure 4.1).

Figure 4.1. Timeline of focal animal behavioural observation period for an individual captive lion-tailed macaque.



The pattern of individual sampling was rotated each day to enable a representative full daily activity budget for each individual to be formed (see Figure 4.2). Observations were carried out for 12 consecutive days thus allowing at least one full rotation of focal animal sampling order to be carried out. This meant that each individual was not sampled at the same time every day and thus by the end of the study, each individual had been sampled for the full duration of each sampling period. The behavioural data was then entered into Excel spreadsheets for analysis. This procedure was repeated for each zoo (in the order described in General methods, Chapter 2, see Figure 2.1)

Figure 4.2. Example of the rotation of individual lion-tailed macaques within a group for behavioural observations.

Time of day	Day 1	Day 2	Day 3	Day 4 .....etc
09:00h – 09:10h	Individual 1	Individual 2	Individual 3	Individual 4
09:10h – 09:20h	Individual 2	Individual 3	Individual 4	Individual 5
09:20h – 09:30h	Individual 3	Individual 4	Individual 5	Individual 1
09:30h – 09:40h	Individual 4	Individual 5	Individual 1	Individual 2
09:40h – 09:50h	Individual 5	Individual 1	Individual 2	Individual 3

This was repeated for the sampling periods 12:00h – 14:00h and 15:00h – 17:00h

4.2.2. Descriptive and statistical analysis of behavioural data

4.2.2.1 Descriptive analysis of behavioural data

For each individual, the percentage of time spent performing each behaviour state as a proportion of the total activity budget, was calculated for each sampling period. These values were then averaged over the 12 days. The three sampling periods were kept separate throughout analysis so that the effects of time of day could be investigated. Group means of the time spent performing state behaviours (%) were calculated so that activity budgets could be represented graphically for each sampling period and for each zoo.

4.2.2.2 Statistical analysis of behavioural data

State behaviours

To assess differences between the duration of behavioural states, normality tests were conducted using one-sample Kolmogorov-Smirnov test in SPSS (version 12.0). As all behaviours were found to be normally distributed, one-way ANOVA tests were performed to investigate differences in state behaviours between the zoos, for each time period. Post hoc analyses in the form of Tukey tests, were performed to determine which zoos differed. Statistical analysis was not carried out on behaviours that were performed for less than 1% of the time. These were, mating, infant suckling, and sex inspection.

Differences in state behaviours between adults and juveniles

Comparisons of state behaviours were made between adults and juveniles, where juveniles were classed as those individuals aged four years and under. Once again, tests for normality were performed using one-sample Kolmogorov-Smirnov test in SPSS (version 12.0). For each zoo, using Minitab (version 12.0), two sample t-tests were performed on behaviours that were normally distributed to investigate

differences in state behaviours between adults and juveniles and between zoos for each time period. Mann Whitney U-tests were performed on non-normally distributed behaviours. Statistical analysis was not carried out on behaviours that were performed for less than 1% of the time. These were, mating, infant suckling, and sex inspection.

Any differences found between zoos and between adults and juveniles were then represented graphically for each zoo and for each sampling period.

Events

No statistical analysis was performed on the event behaviours, as many behaviours were performed infrequently and some behaviours were only performed by certain individuals, so the frequency did not act as a full representation of the group. Graphs were plotted to represent the frequency of event behaviours across the five zoos for each sampling period.

Time of day

To determine how the time of day differed in relation to behaviour between zoos, mixed model analysis was carried out which allows for correlations occurring between repeated observations and this was performed on state behaviours using SAS (Statistical Analysis Software, version 8.2). Tables were then formed that summarized where differences occurred between the sampling periods and zoos for each behaviour and graphs were plotted respectively.

4.3. Results

4.3.1. Variation in activity budgets between zoos for each sampling period

Although the Time spent performing behaviour was averaged across each group, and thus termed mean time spent on behaviour (%). Throughout this chapter it will be shortened to 'time spent exhibiting' a particular behaviour.

4.3.1.1. Variation in state behaviours between zoos for each sampling period

a) 09:00h – 11:00h

Figure 4.3. shows the duration of state behaviours for the sampling period 09:00h – 11:00h. On average groups spent 37.1% (SE ± 3.4) of their time resting, 12.5% (SE ± 5.8) of time foraging, 11.4% (SE ± 2.8) of time feeding and 10.9% (SE ± 2.9) allogrooming. All other behaviours were performed on average for less than 10% of the time. The group at Zoo E spent approximately 25% of their time out of sight of the observer.

When comparing these zoos statistically, significant differences between zoos were found in allogrooming, autogrooming, foraging and locomotion (see below).

Allogrooming differed between zoos (One-way ANOVA, N = 37, DF = 36, S = 8.218, p = 0.005) (see Figure 4.4. a). Tukeys test showed that Zoos D and E spent significantly less time allogrooming compared with Zoos A, B and C.

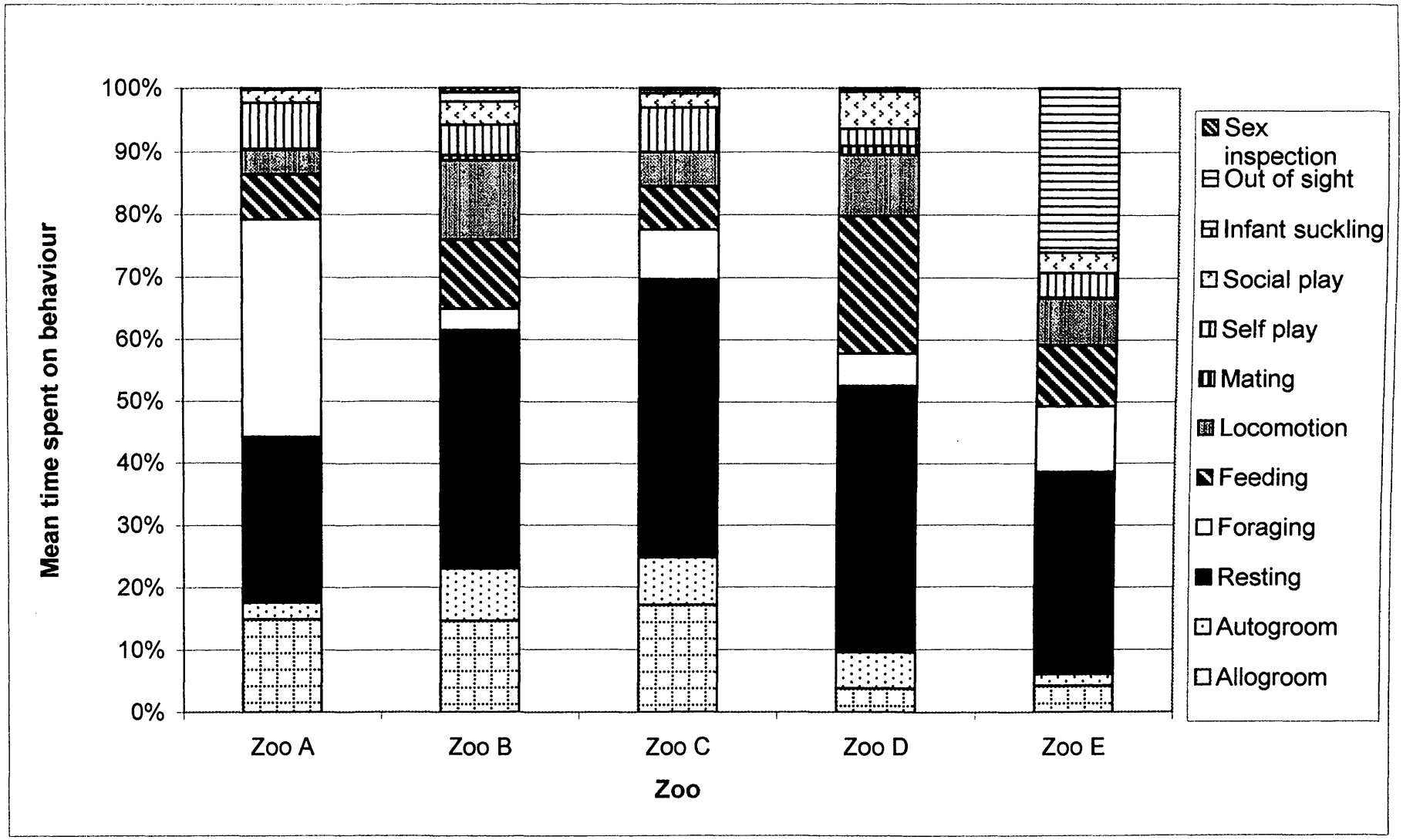


Figure 4.3. The activity budgets of state behaviours exhibited from 09:00h - 11:00h by lion-tailed macaques (*Macaca silenus*) in the captive British and Irish population.

Autogrooming also differed between zoos (S = 0.012, p = 0.012) (see Figure 4.4. b). Tukeys test showed that Zoos A and E spent significantly less time on autogrooming in comparison with zoos B, C and D. Significant differences were found for foraging (S = 8.580, p = 0.000) (see Figure 4.4. c). Tukeys test showed that Zoo A spent a significantly longer time foraging than the other four zoos. Locomotion also differed between zoos (S = 3.357, p = 0.001) (see Figure 4.4. d) where Tukeys test showed that Zoos A and C spent significantly less time on locomotion in comparison with other zoos.

b) 12:00h – 14:00h

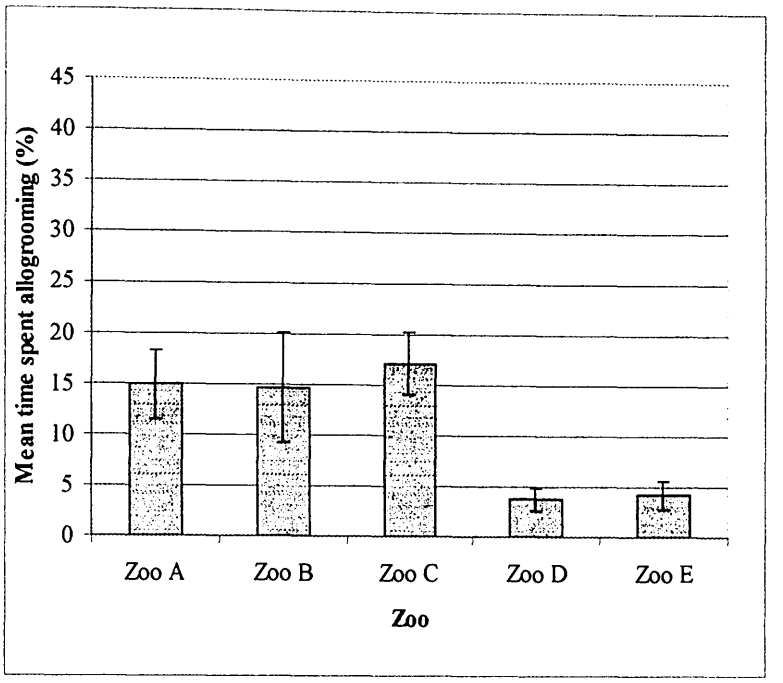
Figure 4.5. shows the duration of state behaviours for the sampling period 12:00h – 14:00h. On average groups spent 36.7% (SE ± 2.0) of their time resting, 15.4% (SE ± 4.9) of their time foraging and 11.6% (SE ± 4.3) feeding. All other behaviours were performed on average for less than 10% of the time.

When comparing these zoos statistically, significant differences between zoos were found in autogrooming, feeding, foraging and locomotion (see below).

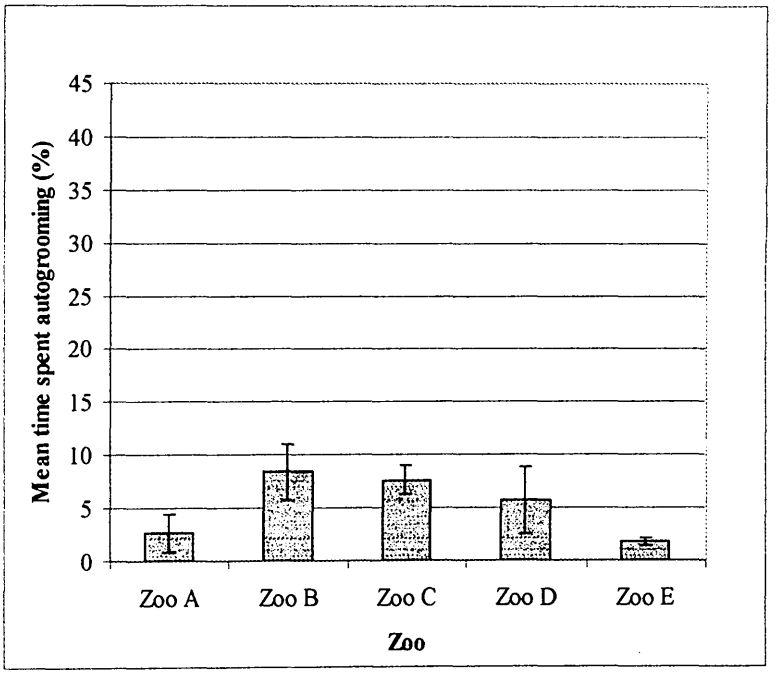
Autogrooming differed between zoos (One-way ANOVA, N = 37, DF = 36, S = 3.229, p = 0.000) (see Figure 4.6. a) where Tukeys test showed that, Zoos A, D and E spent significantly less time autogrooming than Zoos B and C. Feeding also differed between zoos (S = 4.865, p = 0.000) (see Figure 4.6. b). Tukeys test showed that Zoo D spent a significantly longer time feeding than the other four zoos. A significant difference was found in foraging (S = 8.482, p = 0.000) (see Figure 4.6. c) where Tukeys tests showed that Zoos B and C spent significantly less time foraging compared with Zoos A, D and E. Locomotion also differed between zoos (S = 3.722, p = 0.015) (see Figure 4.6. d). Tukeys tests showed that Zoo B spent a longer time on locomotion in comparison with the other four zoos.

Figure 4.4. a, b, c, d. Mean duration (± SE) of state behaviours exhibited by the British and Irish captive population of lion-tailed macaques that showed significant differences between zoos during the sampling period 12:00h – 14:00h.

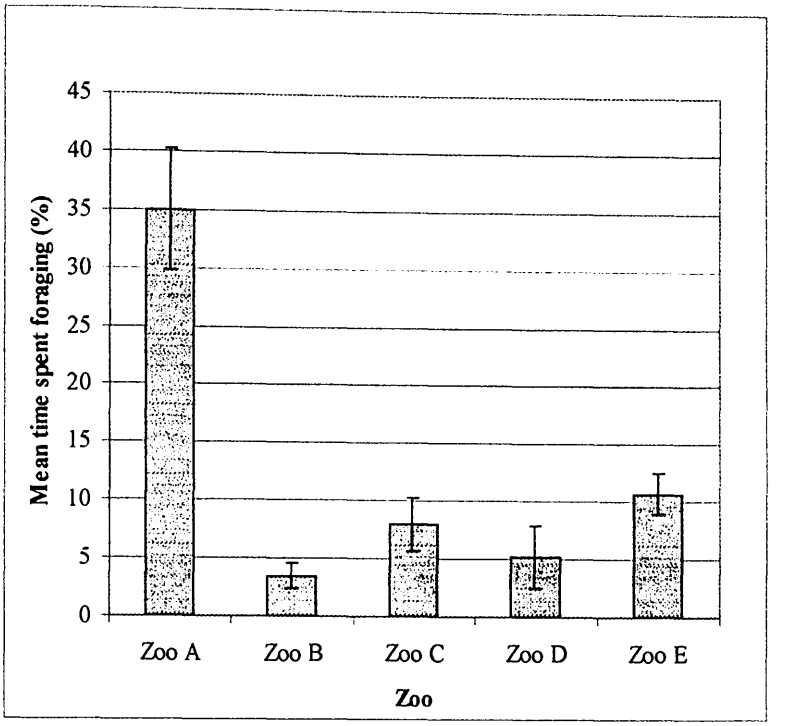
a) Allogrooming during 09:00h – 11:00h



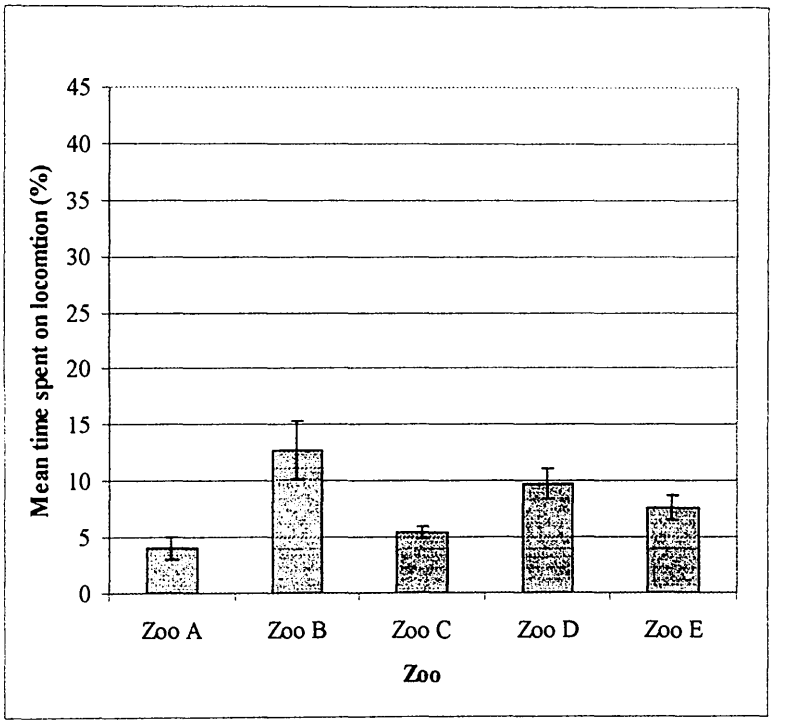
b) Autogrooming during 09:00h – 11:00h



c) Foraging during 09:00h – 11:00h



d) Locomotion during 09:00h – 11:00h



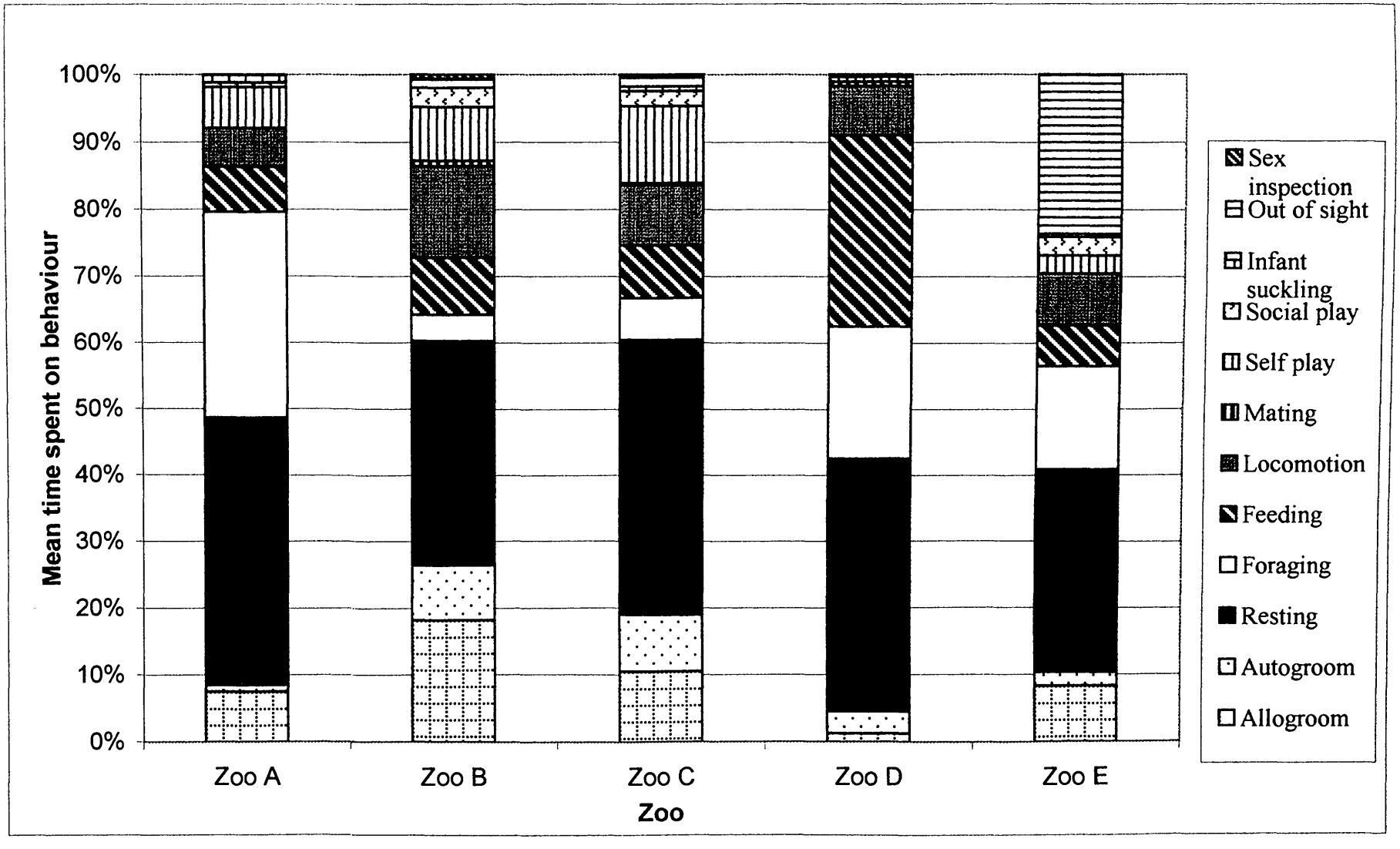
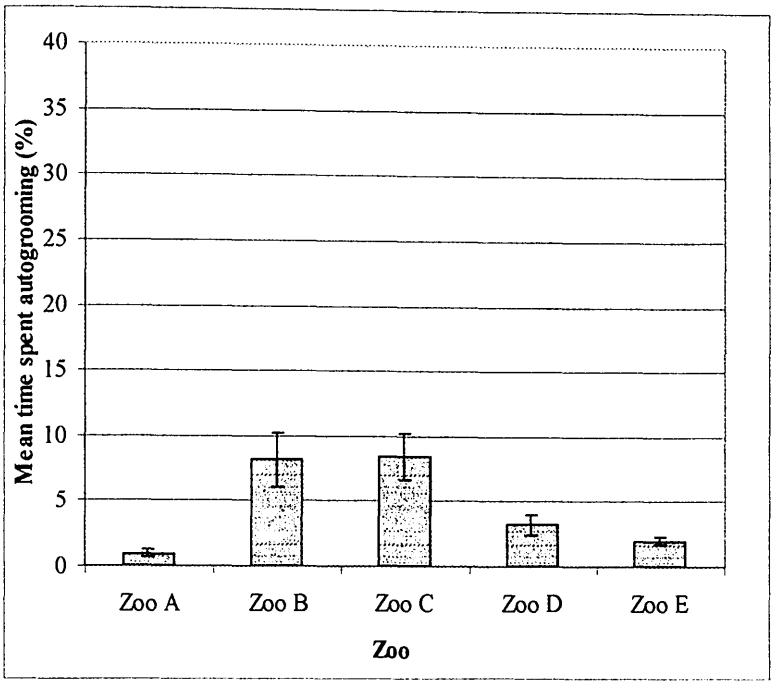


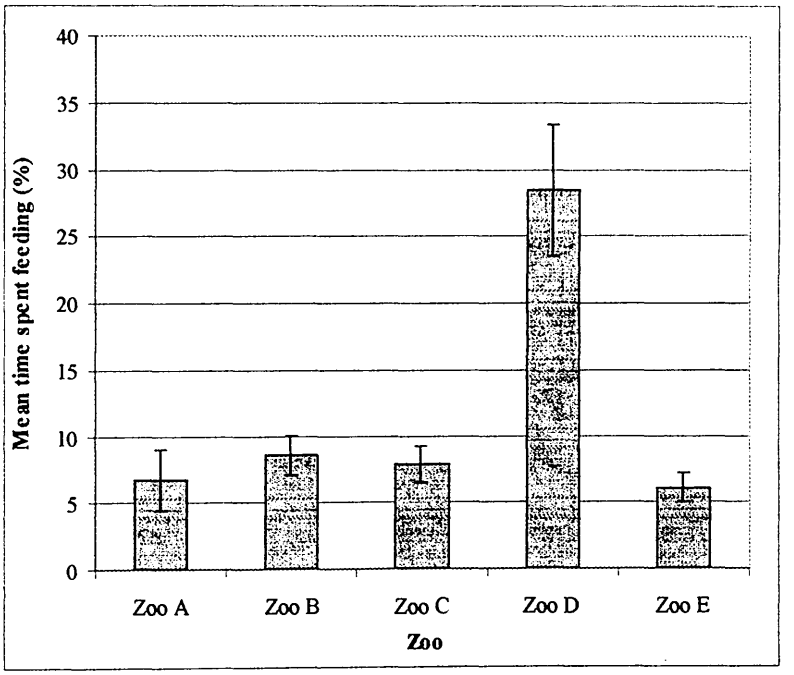
Figure 4.5. The activity budgets of state behaviours exhibited from 12:00h - 14:00h by lion-tailed macaques (*Macaca silenus*) in the captive British and Irish population.

Figure 4.6. a, b, c, d. Mean (± SE) of state behaviours exhibited by the British and Irish captive population of lion-tailed macaques that showed significant differences between zoos during the sampling period 12:00h – 14:00h

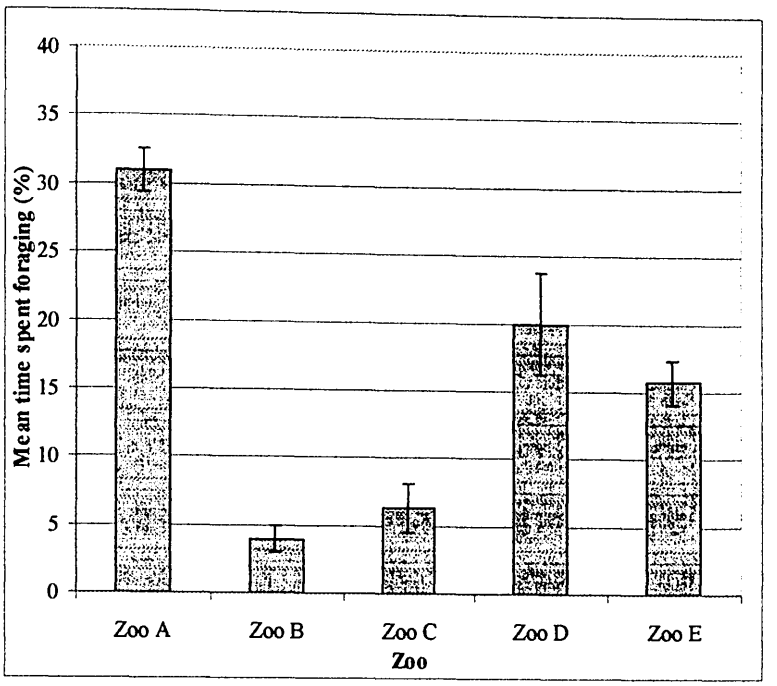
a) Autogrooming during 12:00h – 14:00h



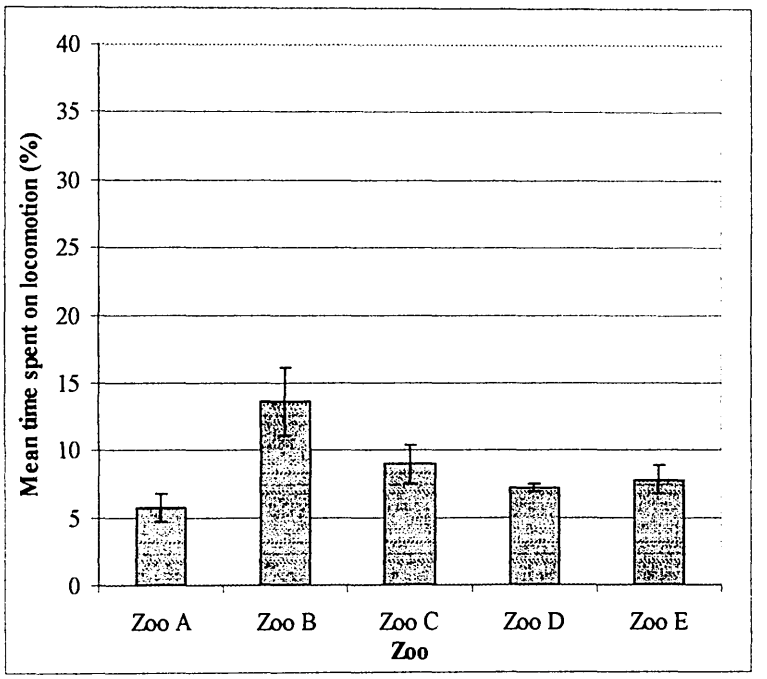
b) Feeding during 12:00h – 14:00h



c) Foraging during 12:00h – 14:00h



d) Locomotion during 12:00h – 14:00h



c) 15:00h – 17:00h

Figure 4.7. shows the duration of state behaviours for the sampling period 15:00h – 17:00h. On average groups spent 30.2% (SE ± 3.8) of their time resting, 15.3% (SE ± 4.1) of their time foraging and 17.0% (SE ± 3.8) feeding. All other behaviours were performed on average for less than 10% of the time.

When comparing these zoos statistically, significant differences between zoos were found in autogrooming, feeding and foraging (see below).

Autogrooming differed between zoos (One-way ANOVA, N = 37, DF = 36, S = 4.402, p = 0.041) (see Figure 4.8. a). Tukeys test showed, that zoo C spent a significantly longer time autogrooming in comparison with zoo E. Significant differences were also found in feeding (S = 5.873, p = 0.000) (see Figure 4.8. b) where Tukeys test showed that Zoo E spent significantly less time feeding compared with the other zoos and Zoo D showed a significantly greater time spent on feeding in comparison with the Zoos B, C and E. Foraging also differed between zoos (S = 10.04, p = 0.001) (see Figure 4.8. c). Tukeys tests showed that Zoo A spent significantly more time foraging in comparison with the other zoos.

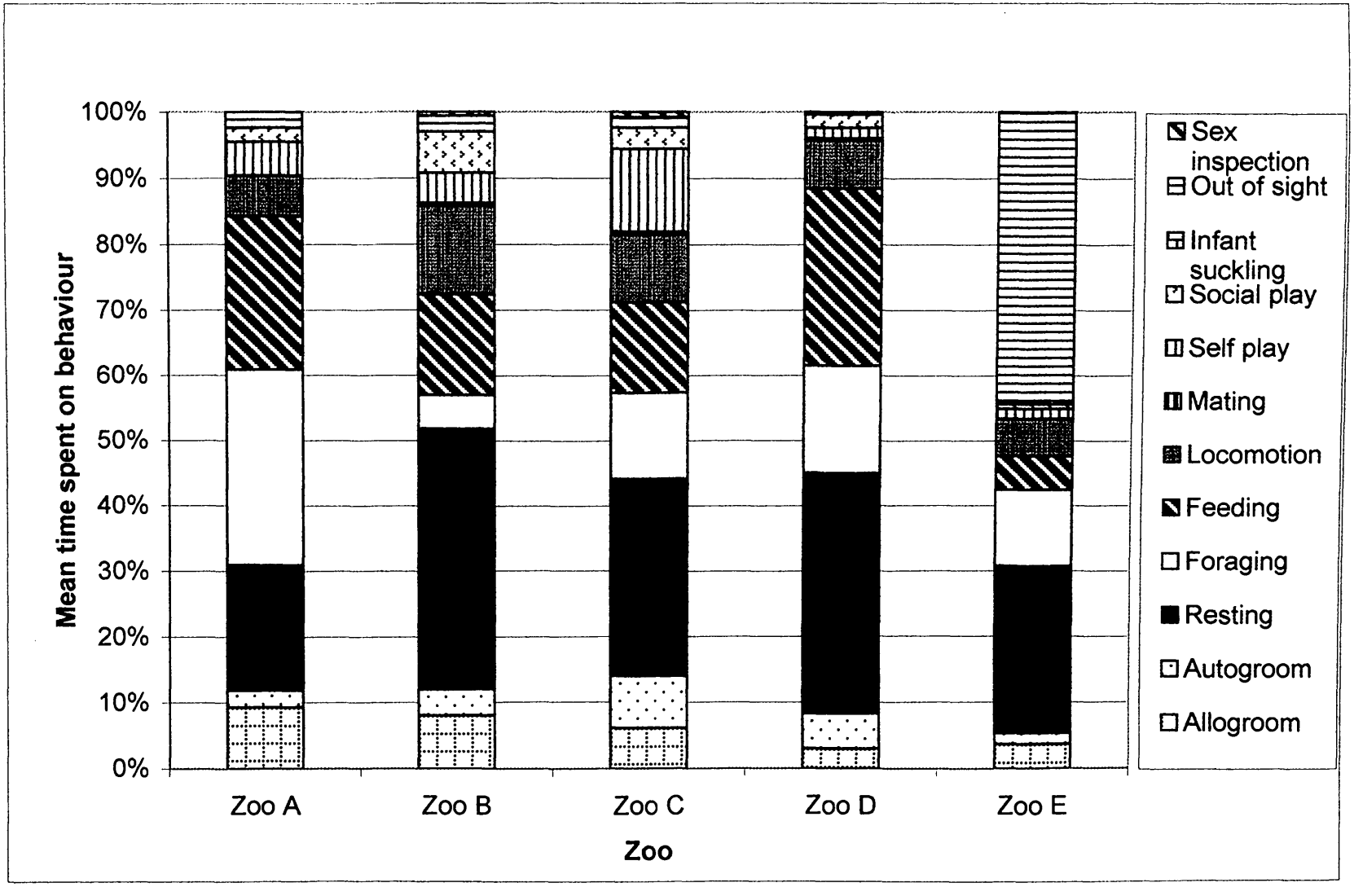
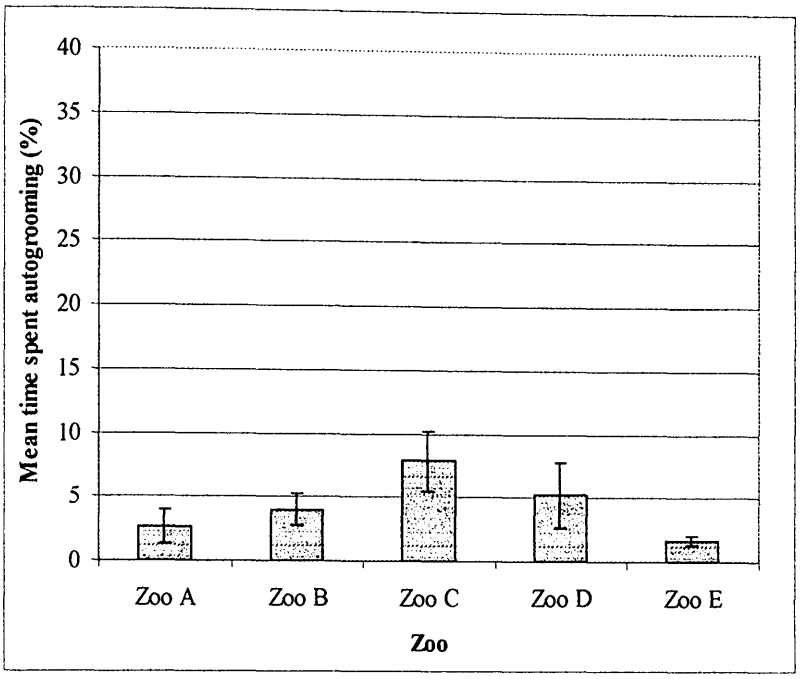


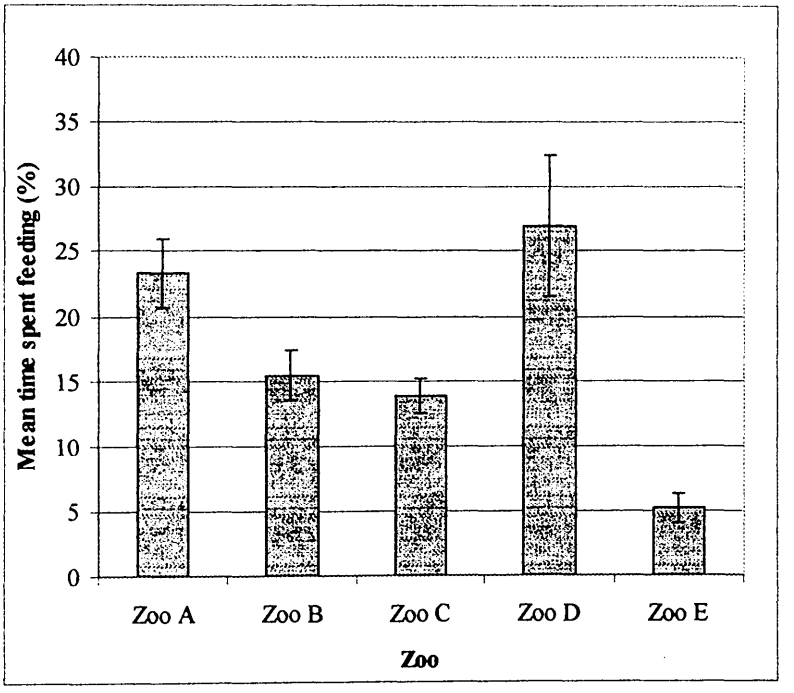
Figure 4.7. The activity budgets of state behaviours exhibited from 15:00h - 17:00h by lion-tailed macaques (*Macaca silenus*) in the captive British and Irish population.

Figure 4.8. a, b, c, d. Mean (±SE) state behaviours exhibited by the British and Irish captive population of lion-tailed macaques that showed significant differences between zoos during the sampling period 15:00h – 17:00h

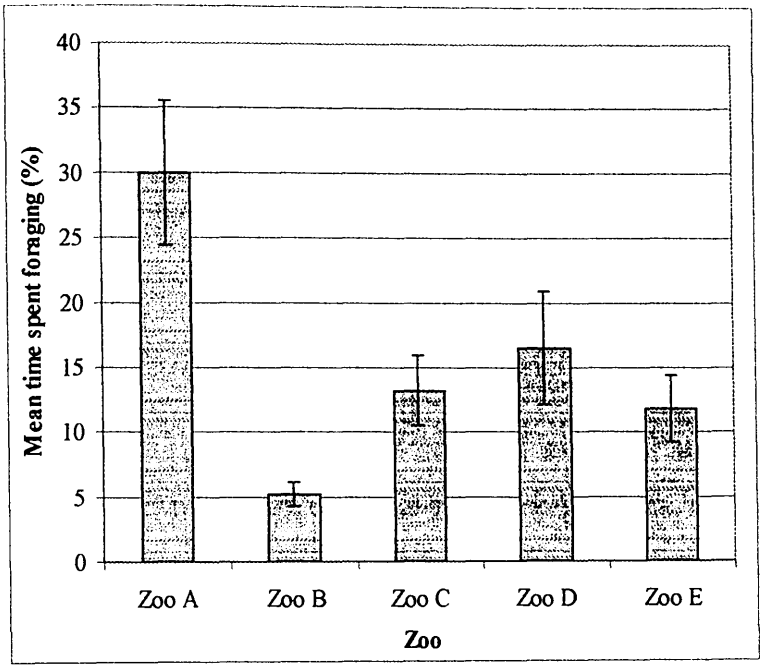
a) Autogrooming during 15:00h – 17:00h



b) Feeding during 15:00h – 17:00h



c) Foraging during 15:00h – 17:00h



4.3.1.2. Variation in event behaviours between zoos for each sampling period

No statistical analysis was performed on the event behaviours, as many behaviours were performed infrequently and some behaviours were only performed by certain individuals, so the frequency did not act as a full representation of the group.

a) 09:00h – 11:00h

The frequency of event behaviours varied considerably between zoos (see Figure 4.9.). For the sampling period 09:00h – 11:00h, the two most noticeable variations were in the frequency of contact calls and grunt vocalizations, where Zoo D appeared to have the greatest frequency in both these vocalizations in comparison with other zoos.

Zoo B exhibited the highest frequency of growl vocalizations for this sampling period. Few differences between zoos in other event behaviours were observed. 'Hand to eye' behaviour was only present in three of the zoos (Zoos A, B and E) and was only performed by three individuals, thus was of low frequency but occurred most frequently during the sampling period 09:00h –11:00h.

b) 12:00h – 14:00h

For the sampling period 12:00h – 14:00h (see Figure 4.10) Zoo D once again had the highest frequency of contact calls and Zoo B had the highest frequency of grunt vocalizations. The frequency of mounting appeared to be highest during the 12:00h – 14:00h sampling period for Zoos A, B and C. Appeasement facial displays, threat facial displays, aggression and squeal vocals showed the highest frequency in all zoos during the sampling period 12:00h – 14:00h

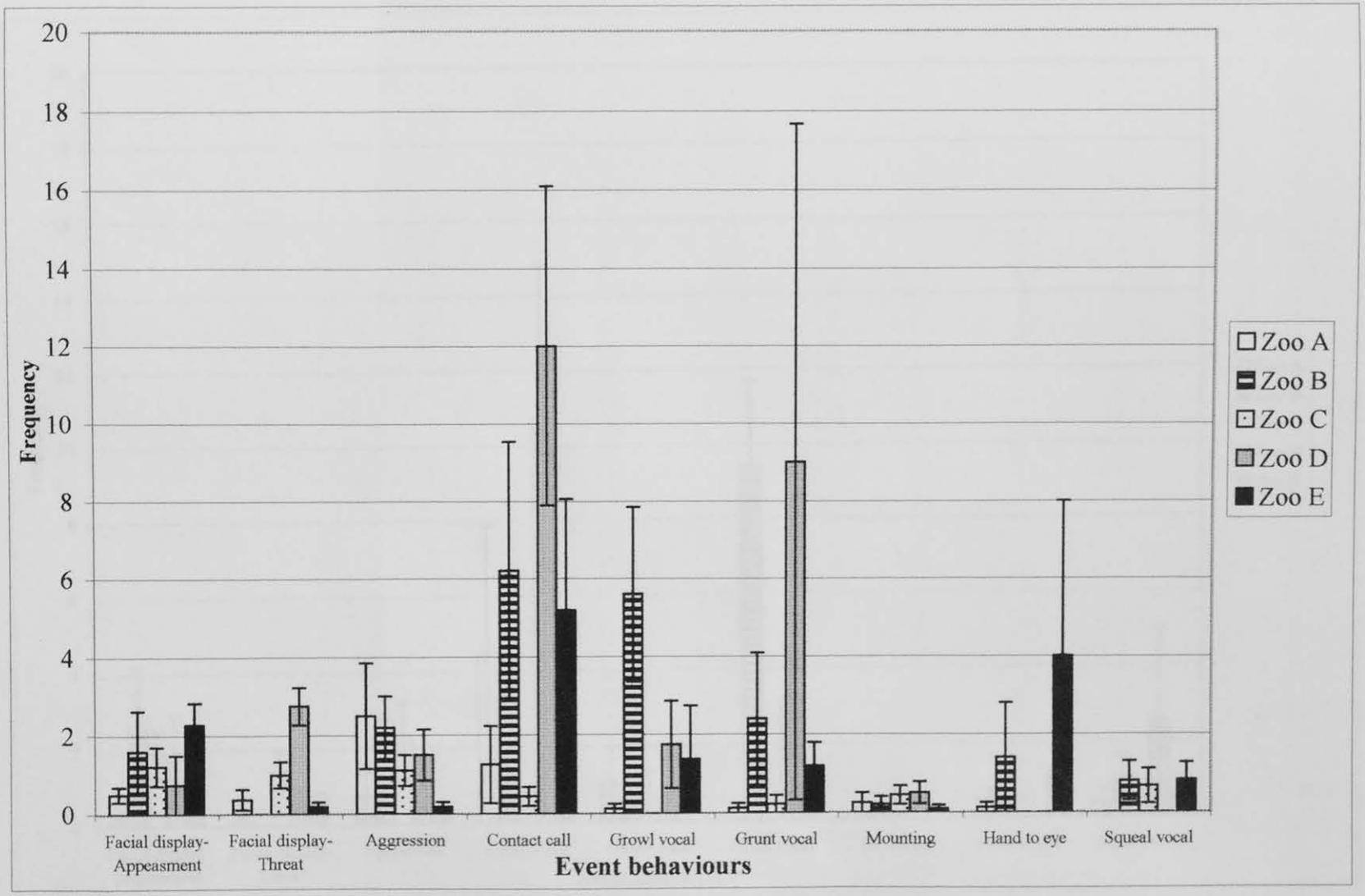


Figure 4.9. Mean (+/- SE) event behaviours exhibited by the captive British and Irish population of lion-tailed macaques (*Macaca silenus*) from 09:00h - 11:00h.

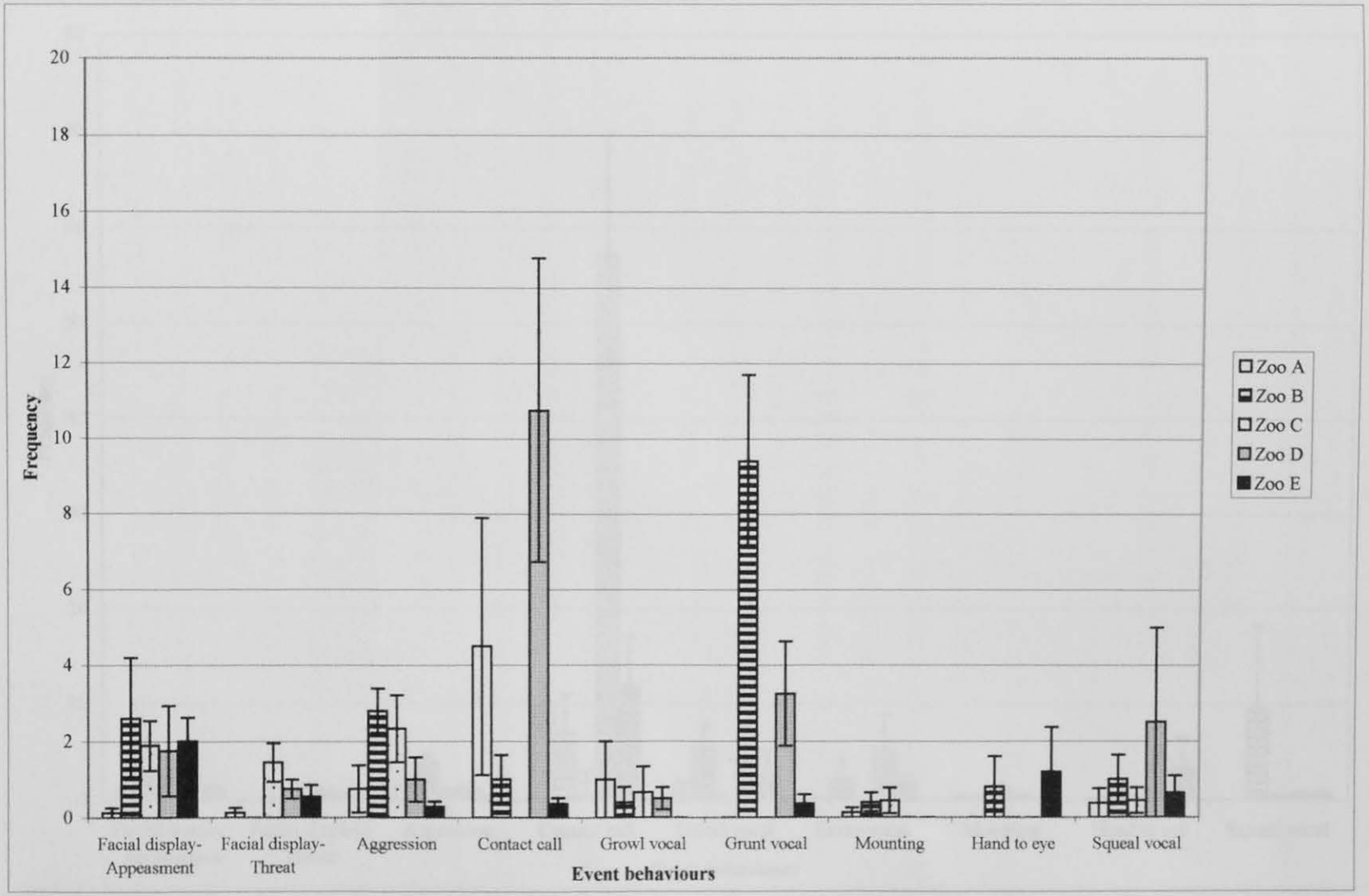


Figure 4.10. Mean (+/- SE) event behaviours exhibited by the British and Irish captive population of lion-tailed macaques (*Macaca silenus*) from 12:00h - 14:00h.

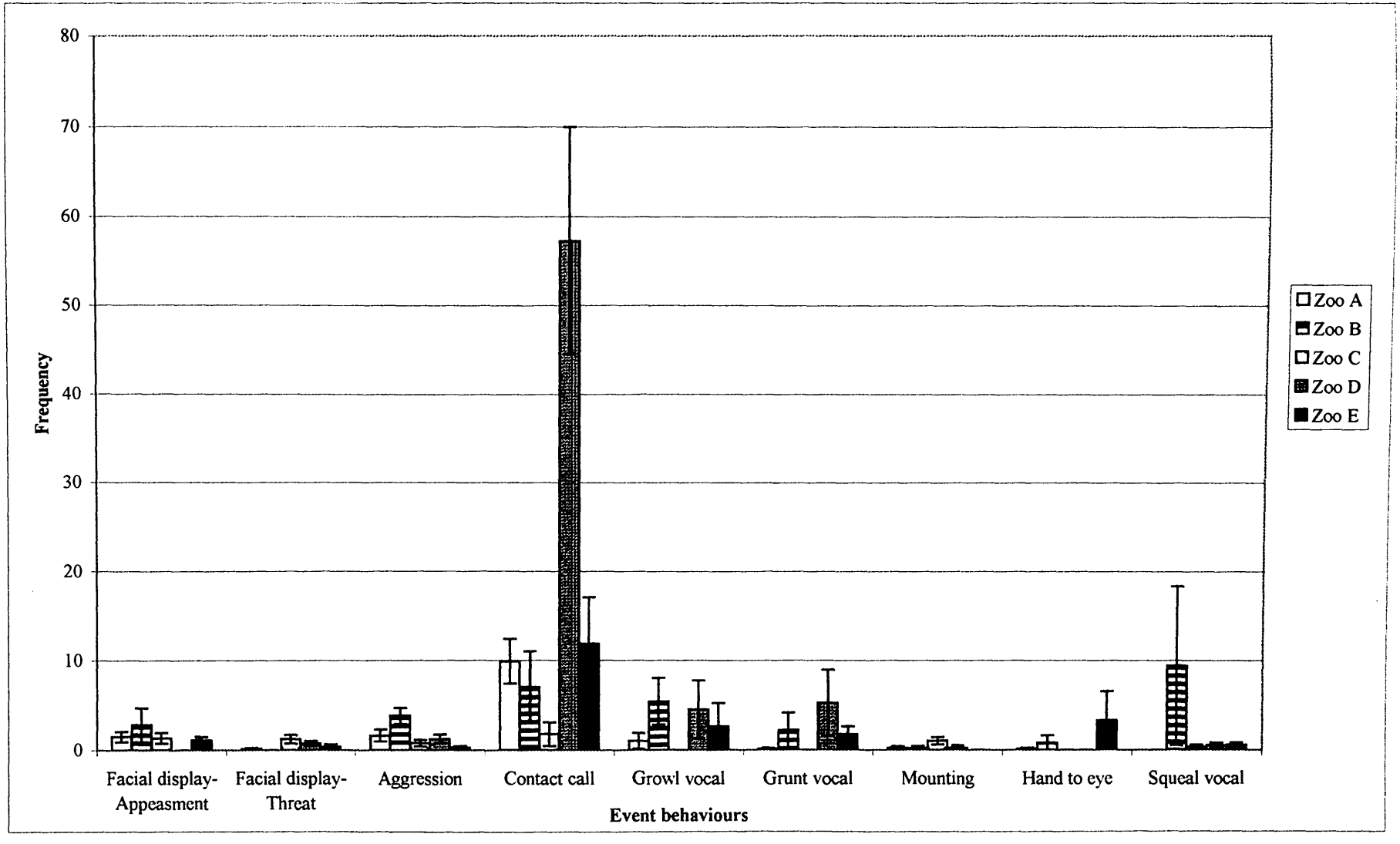


Figure 4.11. Mean (+/- SE) event behaviours exhibited by the captive British and Irish population of lion-tailed macaques (*Macaca silenus*) from 15:00h - 17:00h.

c) 15:00h – 17:00h

In the sampling period 15:00h – 17:00h (see Figure 4.11) the only noticeable difference was in contact calls, where once again Zoo D elicited a much higher frequency in comparison with the other zoos and overall the frequency of this call was very high compared to the other sampling periods.

4.3.2. Differences in state behaviours between adult and juveniles

a) 09:00h – 11:00h

Figure 4.12. shows the duration of state behaviours for both adults and juveniles for the sampling period 09:00h – 11:00h. On average, adults spent 14.29% (SE ± 2.1) of their time allogrooming, 41.24% (SE ± 3.4) of their time resting, 15.54% (SE ± 3.6) of their time foraging and 10.5% (SE ± 2.5) of their time feeding. On average, juveniles spent 29.5% (SE ± 3.2) of their time resting, 11.34% (SE ± 2.5) of their time foraging, 12% (SE ± 2.8) of their time on self play. All other behaviours were performed on average for less than 10% of the time.

When comparing between behaviours exhibited by adults and juveniles, significant differences were found in allogrooming, resting, locomotion, self play and social play (see below and Figure 4.12). Statistical analysis was not carried out on the time spent mating, infant suckling and sex inspection, as these behaviours were performed on average for less than 1% of time.

Adults spent more time than juveniles on allogrooming (Two sample t-test, N = 21 and 16 respectively, T = 2.58, p = 0.014) and resting (T = 2.52, p = 0.017). However, juveniles spent more time than adults on locomotion (T = -2.76, p = 0.010), self play (Mann-Whitney U, N = 16 and 21 respectively, W = 238.5, p = 0.000) and social play (W = 235.5, p = 0.000).

No differences between adults and juveniles were found in any of the other behaviours.

b) 12:00h – 14:00h

Figure 4.13. shows the duration of state behaviours for both adults and juveniles for the sampling period 12:00h – 14:00h. On average, adults spent 13.26% (SE ± 2.3) of their time allogrooming, 41.90% (SE ± 2.4) of their time resting, and 18.09% (SE ± 11.9) of their time foraging. On average, juveniles spent 30.07% (SE ± 3.0) of their time resting, 11.87% (SE ± 2.2) of their time foraging, 10.8% (SE ± 1.3) of their time on locomotion and 13.8% (SE ± 2.4) of their time on self play. All other behaviours were performed on average for less than 10% of the time.

When comparing between behaviours exhibited by adults and juveniles, significant differences were found in allogrooming, resting, locomotion, self play and social play (see below and Figure 4.13).

Adults spent more time than juveniles on allogrooming (Two sample t-test, N = 21 and 16 respectively, T = 3.68, p = 0.001) and resting (T = 3.30, p = 0.017). However, juveniles spent more time than adults on locomotion (T = -3.42, p = 0.003), self play (Mann-Whitney U, N = 16 and 21 respectively, W = 249.5, p = 0.000) and social play (W = 249.5, p = 0.000).

No differences between adults and juveniles were found in any of the other behaviours.

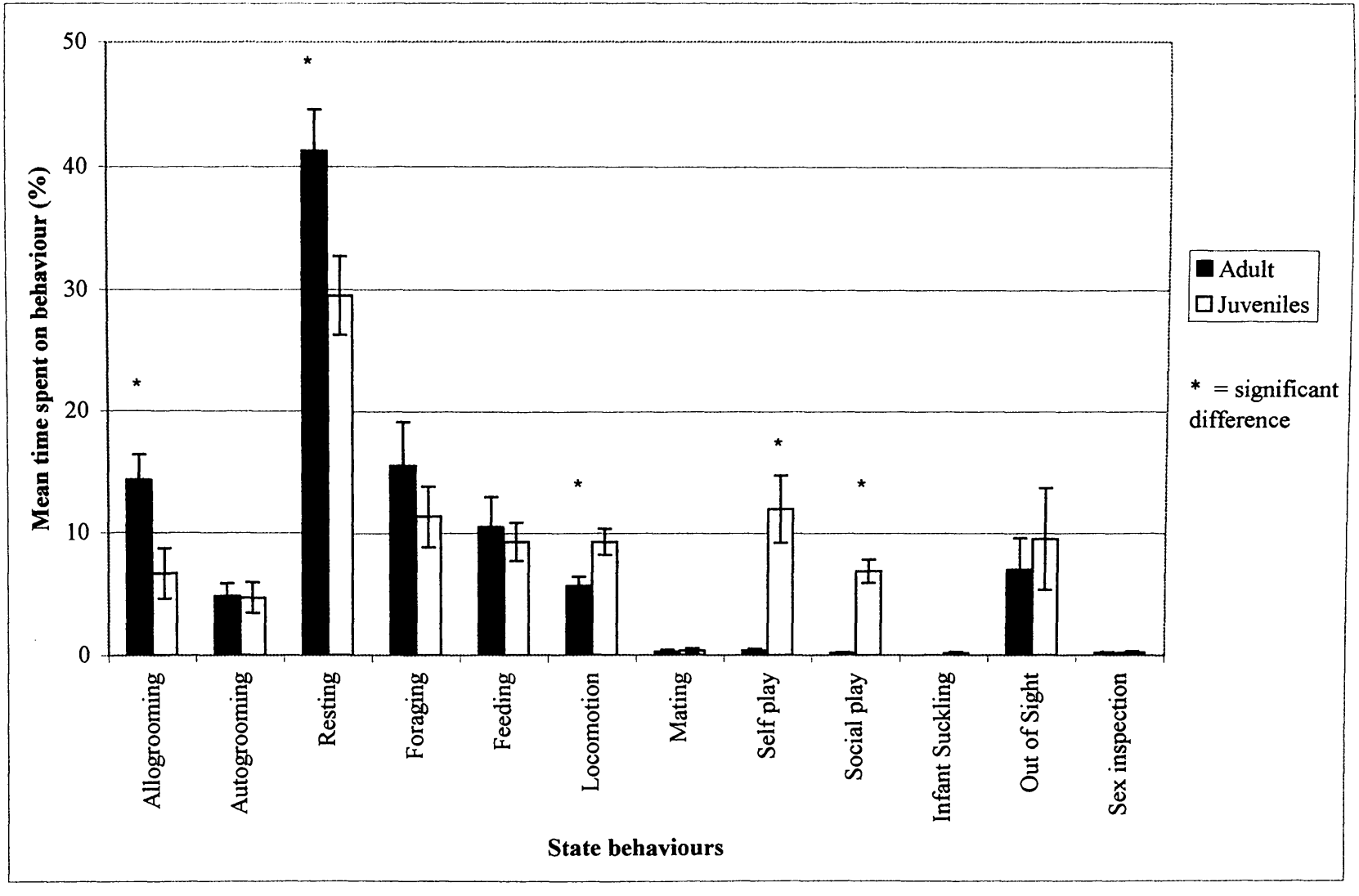


Figure 4.12 The activity budgets of state behaviours exhibited from 09:00h - 11:00h by adult and juvenile lion-tailed macaques (*Macaca silenus*).

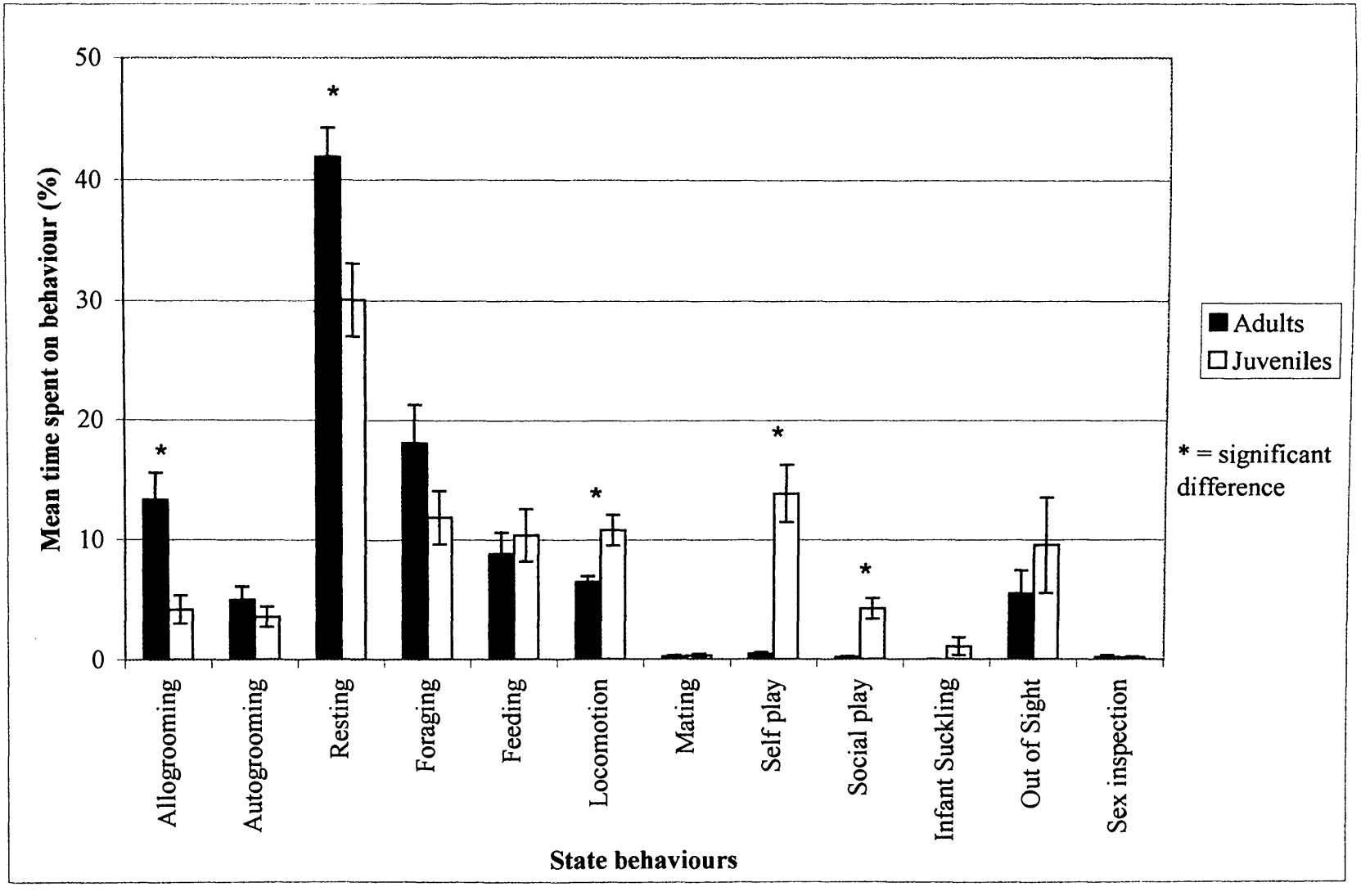


Figure 4.13. The activity budgets of state behaviours exhibited from 12:00h - 14:00h by adult and juvenile lion-tailed macaques (*Macaca silenus*).

b) 15:00h – 17:00h

Figure 4.14. shows the duration of state behaviours for both adults and juveniles for the sampling period 15:00h – 17:00h. On average, adults spent 35.01% (SE ± 3.4) of their time resting, 18.76% (SE ± 3.1) of their time foraging and 13.71% (SE ± 2.0) of their time feeding. On average, juveniles spent 19.5% (SE ± 2.0) of their time resting, 11.69% (SE ± 2.3) of their time foraging, 16.63% (SE ± 2.5) of their time feeding, 11.44% (SE ± 1.7) of their time on locomotion and 11.91% (SE ± 2.7) of their time on self play. All other behaviours were performed on average for less than 10% of the time.

When comparing between behaviours exhibited by adults and juveniles, significant differences were found in allogrooming, autogrooming, resting, locomotion, self play and social play (see below and Figure 4.14).

Adults spent more time than juveniles on allogrooming (Two sample t-test, $N = 21$ and 16 respectively, $T = 3.12$, $p = 0.004$), autogrooming ($T = 2.25$, $p = 0.033$) and resting ($T = 3.98$, $p = 0.000$). However, juveniles spent more time than adults on locomotion ($T = -3.26$, $p = 0.004$), self play (Mann-Whitney U, $N = 16$ and 21 respectively, $W = 243$, $p = 0.000$) and social play ($W = 250$, $p = 0.000$).

No differences between adults and juveniles were found in any of the other behaviours.

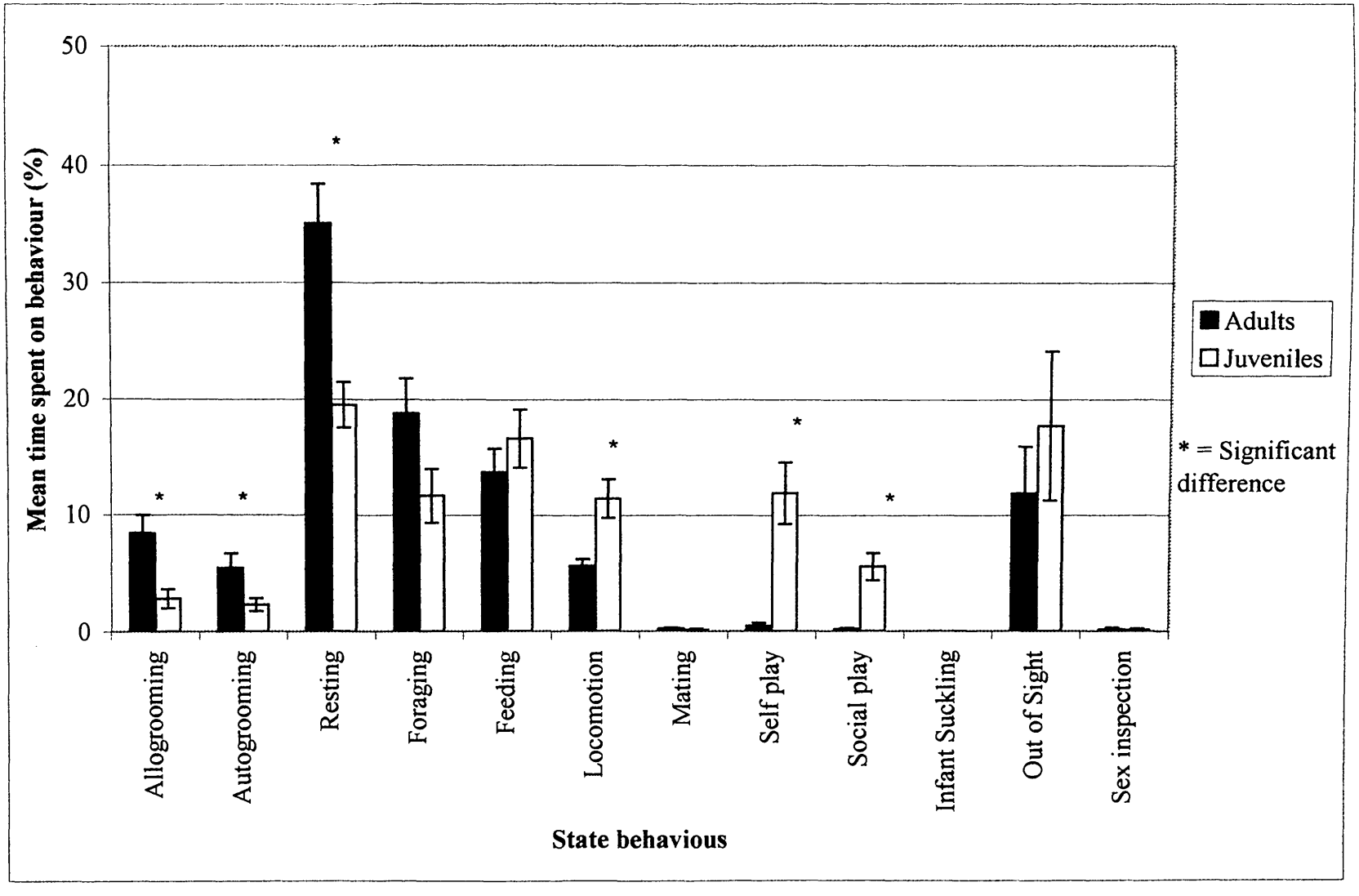
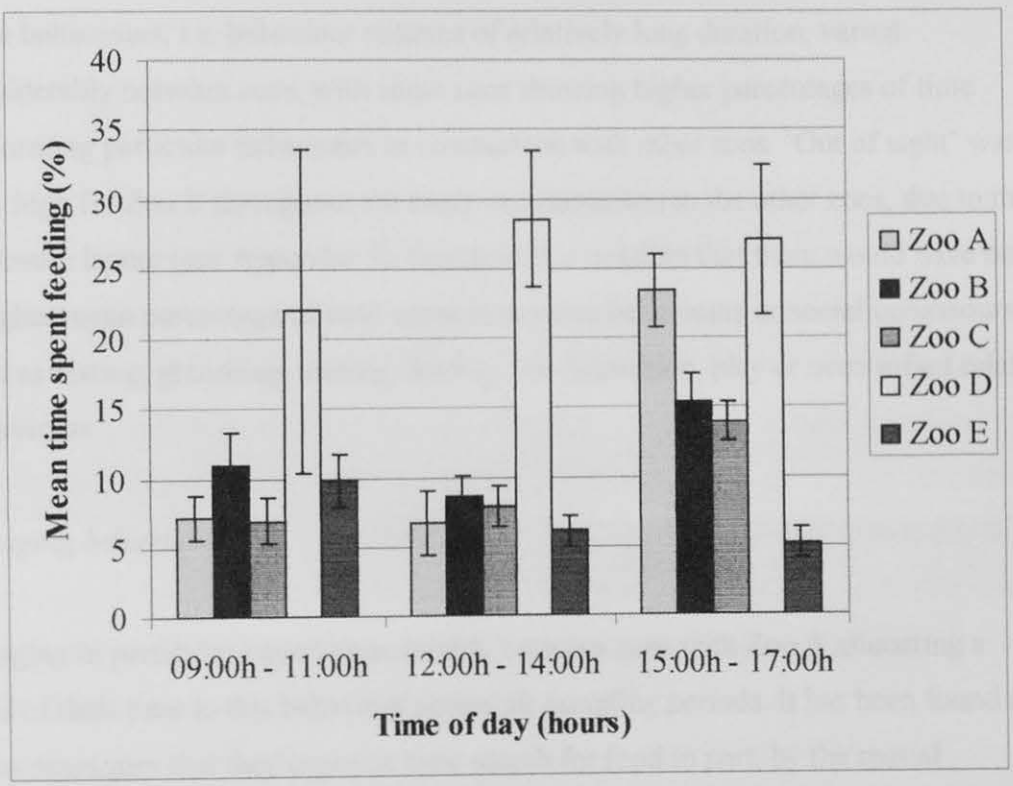


Figure 4.14. The activity budgets of state behaviours exhibited during 15:00h - 17:00h by adult and juvenile lion-tailed macaques (*Macaca silenus*).

4.3.3. The effect of time of day on the behaviour exhibited by captive lion-tailed macaques

Only one significant result was found. It appears that time of day significantly influenced feeding behaviour ($F = 3.76$, $p = 0.0007$). Overall, feeding behaviour (see Figure 4.15) was highest in the afternoon (15:00h – 17:00h) and lowest at midday (12:00h – 14:00h). Zoo D spent a longer time feeding in comparison with the other zoos and the time spent feeding seemed to decrease slightly after midday. Zoos A and B showed a decrease in feeding towards midday, but this then increased in the afternoon (15:00h – 17:00h). Zoo E showed the lowest overall percentage time spent feeding and this decreased throughout the day.

Figure 4.15. The influence of time of day on the mean (±SE) time spent feeding (%) in the British and Irish captive population of lion-tailed macaques.



4.4. Discussion

Animals in the wild are, as expected, strongly influenced by environmental influences such as predation and availability of resources. The common view is that these animals are "free", however, their behaviour and use of space are substantially restrained by their surroundings (Hediger, 1950). The constraints of the captive environment are more salient than those in the wild and often include extreme restrictions on available space and resources, preventing some species from exhibiting their full range of natural behaviours while in captivity (Lukas *et al*, 2003). In recent years, modifications in captive environments have occurred, to expand behavioural opportunities and increase the probability that animals will retain species-specific behavioural competence (Redshaw & Mallinson, 1991).

Variation in state behaviours between zoos

State behaviours, i.e. behaviour patterns of relatively long duration, varied considerably between zoos, with some zoos showing higher percentages of time performing particular behaviours in comparison with other zoos. 'Out of sight' was very high for Zoo E throughout the study in comparison to the other zoos, due to the enclosure layout (see Appendix 3), therefore it is possible that there would have been a higher mean percentage of time spent in inactive behaviours or social behaviours, such as resting, grooming, mating, feeding, sex inspection, play or even infant related behaviours.

Foraging behaviour

Foraging in particular varied considerably between zoos with Zoo A allocating a third of their time to this behaviour across all sampling periods. It has been found in some macaques that they organize their search for food in part, by the spatial proximity of food items to environmental structures, or by organizing their investigations primarily by the distance from the food location (Menzel, 1996). Menzel's (1996) work on foraging in long-tailed macaques (*Macaca fascicularis*)

found that captive born macaques found hidden food more often and more quickly along visible environmental borders and within matching objects than along invisible straight lines. Indeed this correlated with what was observed at Zoo C, where the group followed the same foraging circuit (led by the dominant male) around their outdoor island and very rarely did they actually follow a straight line down the middle of the island.

Lindburg (1998) described foraging as "an elaborate, multi-stage behaviour comprising appetitive (goal-seeking) and consummatory (goal-satisfying) phases. Appetitive components include locating, selecting, gathering or capturing, and processing food items, whereas food ingestion is consummatory behaviour". When an animal is unable to perform both appetitive and consummatory components of complex natural behaviours such as foraging, its physiological and psychological welfare may suffer. A prime example is the restriction of a captive animal's appetitive foraging opportunities because of being fed an easily consumed commercial diet provided in predictable spatial and temporal locations (Jones & Pillay, 2004).

In a wild protected population of lion-tailed macaques, it was found that foraging was the third most common activity, where they spent 26.7% of their time performing this activity and in fragmented populations (i.e. isolated populations) the proportion of activity budget allocated to foraging was 23.7% (Menon & Poirier, 1996). Thus, Zoo A with an average of 33% seems to conform to wild protected populations. However, the remaining four zoos showed in general a mean time spent foraging of 10-15% possibly indicating consequences of a restricted habitat due to captivity and thus posing implications for wild fragmented populations. In this study it appeared that the available type of foraging substrate strongly influences the time spent foraging and thus poses possible welfare implications as suggested by Jones & Pillay (2004), however, this will be discussed in detail in Chapter 5.

Feeding

Food acquisition is one of the most important preoccupations in an animals' life, with diet accounting for most of the ecological and behavioural differences among primate species (Singh *et al*, 2000). In this study it was found that the mean time spent feeding was similar between zoos (ranging from 5 – 15%) with the exception of Zoo D where animals allocated a significantly higher proportion of their time to feeding (20-30%). This was mostly due to a natural abundance of unripe horse chestnuts (*Aesculus hipocastanaceae*), which appeared to be favoured by all the macaques in this group were continuously fed on when no other food was on offer. In comparison, the time spent feeding in wild populations has been reported as on average 27.8% in protected forests and 17.9% in fragmented forests (Menon & Poirier, 1996), therefore the majority of zoos conform to what has been observed in fragmented populations.

It is the aim of zoos to provide a species with a diet that closely mimics the nutritional requirements of their wild counterparts. The diet of lion-tailed macaques was similar between zoos (see Chapter 2, Table 2.2) and all zoos supplemented this diet with live locusts and mealworms to increase their intake of insects. However, the type of foraging substrate provided is likely to have influenced the diet of these macaques, as it was expected that those zoos providing enclosures with a high abundance of grass increased the proportion of insects that the macaques ingested. Therefore, it would be predicted that the nutrition of macaques being housed in less favourable conditions with little foraging substrate such as Zoos B and D would be lacking in some nutrients in comparison with a zoo housing macaques with a great expanse of foraging material, such as Zoos A, C and E. Interestingly, Zoos A, C and E had a higher reproductive success compared with Zoos B and D, however, it is only speculative whether the diet of the macaques really has any influence, considering that other factors also affect the reproductive rate as already discussed in Chapter 3. Macaques at Zoos A, C and E also caught birds or rodents fairly regularly (at least every second day), therefore this added to their overall nutritional intake and

indeed in the wild extra items such as birds, frogs and occasionally bats are part of the lion-tailed macaques diet (Singh *et al*, 2000).

Locomotion

Apart from during the afternoon sampling period, locomotion appeared to significantly differ between zoos with Zoo B showing the highest mean time spent (%) exhibiting this behaviour and consequently significantly differed in relation to the other zoos. Interestingly, this zoo spent the lowest time to foraging and had the least foraging substrate therefore although the group was active it does indicate that they were spending time moving around their enclosure and not actually searching for food. It was noted that they were active more frequently when waiting to be fed and feeding times tended to be the same every day. Whether this was a significant influence will be discussed in Chapter 5. Zoos A, C, D and E spent 5 - 10% of their time on locomotion whereas Zoo B on average spent 10-15% of their time on locomotion. Wild populations in comparison were found to spend 34% on average of their time on locomotion in fragmented populations and only 15% in protected populations (Menon & Poirier, 1996), thus in this case, captive macaques appear to spend a similar amount of time on locomotion in comparison with wild protected populations. Although wild fragmented groups have more space in comparison to a captive situation, they will have to spend more time searching for food as the area is so restricted and some food resources may only be seasonal, but whether the actual size of the enclosure influences the time exhibiting locomotion will be discussed in Chapter 5.

Resting

Resting accounted for 30-50% of the activity budget exhibited by all zoos and it did not significantly differ between any of the zoos. However, in comparison with wild populations, lion-tailed macaques in captive populations appear to rest much more. It was found that in protected forests the macaques allocated 27.8 % of their time to resting, whereas in fragmented populations, this had decreased to 16% (Menon &

Poirier, 1996). Obviously there is no risk of predation in captivity and lion-tailed macaques have more of a daily routine, therefore there are certain times of day when the macaques are not disturbed by feeding and husbandry routines or by visitors and thus the macaques are normally resting during this period. The effect of time of day on resting will be discussed further on in this chapter.

Grooming

Allogrooming has been described for a number of mammalian species and has two main functions. The first function is the removal of ectoparasites from body areas that the animal is not able to reach itself, and secondly, for the maintenance or establishment of social relationships (Lazaro-Perea *et al*, 2004). It has been shown that higher-ranking females primates receive more grooming than they give and more grooming than expected occurs between females who are close in rank (Scino, 2001). Indeed, allogrooming was significantly lower in Zoo D in comparison with the other zoos and this was probably due to the fact that the two females were unrelated. Consequently the time allocated to autogrooming was higher than allogrooming for this zoo. Zoo E showed low levels of grooming in comparison with other zoos, but this could be due to the high proportion of individuals being out of sight during this study, thus it is probable that the rate of grooming would be higher at this zoo.

Play

Play is a complex behaviour and despite the potential benefits for the development of social, cognitive and motor skills, play behaviour does have costs, such as energy expenditure, and the risks of injury and predation (de'Oliveira *et al*, 2003). It has been suggested that play behaviour may be an indicator of habitat quality (Sommer & Mendozagranados, 1995). In this study it was found that play behaviour varied between zoos but this was mainly due to the social structure of the groups as some groups had more juveniles than others. For example, self-play appeared to be the highest at Zoo C, which was unusual as this group had a high number of juveniles and infants in comparison with the other zoos. This group, however, did spend a high

proportion of their time self-playing and this was possibly due to the vast range of enrichment within the enclosure. It was also noted at this zoo that the dominant male interacted more with the youngsters and was involved in social play and this was not observed at any of the other zoos. Social play, however, was high at Zoo D where there were just two juveniles but almost sub adult males present, who were continuously testing each other's strength and at Zoo B where there was just two juveniles of different sex but similar ages. It has been stated that there appears to be a sex bias in relation to play behaviour. It was found in rhesus macaques that male infants exhibited more rough-and-tumble play than female infants and also exhibited more stationary play, chasing play, and initiated play more frequently than female infants (Brown & Dixson, 2000). This correlates with what has been found in this study, for instance as already stated a high level of social play was found at Zoo D where the juveniles were both males and at Zoos A and B there was just one male and one female juvenile and in the majority of cases the male initiated play.

Although no significant differences were found in play behaviour between zoos, it is likely that significant differences occurred between adults and juveniles, which will be discussed later in this chapter. In regards to habitat quality, it was found that play was a sensitive indicator of habitat quality for wild Hanuman langur monkeys (*Presbytis-entellus*) where individuals that were in a poor habitat played less, and this was correlated with the low energy from the poor quality leaves within that habitat. It is possible that the time spent playing may be higher in wild populations that live in a protected forest than those that occupy fragmented forests due to differences in the availability of food, as in fragmented populations individuals would have to spend more time foraging for highly nutritious food and consequently less time would be spent resting or playing. As the captive population receives the optimum diet that is set for this species, then comparison cannot be made.

Sexual activity

Sexual behaviours such as mating and sexual inspection varied between zoos due to the fact that two zoos (Zoos A and D) did not have a dominant male, however Zoo D

did have two juvenile almost sub adult males, one of which the zoo staff are hoping will become dominant. Zoo B showed the highest rate of mating, but this could partly be due to the female advertising oestrus at the time of study. In the wild populations, 'mating couples' have been observed at distances of 100-200m from their group (Fa & Lindburg, 1996). These distances however cannot be copied in a captive situation and the macaques have the additional pressure of the presence of visitors, therefore it is possible that mating would be higher if macaques lived in larger but more secluded enclosures. The recorded time allocated to mating would have been higher if a longer study was conducted at each zoo, due to the oestrus cycles of the females.

Infant related behaviours

The only data collected in regards to mother-infant interactions was when the infant was suckling, as this was a behaviour that could have a long duration. In general, most interactions between mother and infant were allogrooming, resting and suckling. The mothers spent a lot of time allogrooming their infants but, purely from observations, as expected this seemed to decrease as the infant got older. Mothers were also found to play with their infants by lifting the infant above their heads and this seemed to be an instinctive 'game' between all mothers and infants.

Variation in event behaviours between zoos

The frequency of event behavours (i.e. behaviours of relatively short duration) did vary considerably between zoos, although as stated previously the frequencies were of too low numbers for statistical analysis. As these behaviours are of short duration some behaviours may have been missed therefore continuous sampling methods would be better for analysing the frequency of behavioural events.

Many studies regarding the vocalizations of non-human primates have found that alarm calls can elicit behaviourally adaptive responses and consequently when analysing the vervet monkey (*Cercopithecus aethiops*) alarm call system it was said to be 'functionally referential', providing information about both external objects and events (Hauser, 1996). Referential signalling has also been found in rhesus monkeys during agonistic interactions, in which individuals produced five acoustically distinct vocalizations. The acoustics varied in relation to the rank, kinship and probability of receiving physical contact and thus were used to recruit aid from other members of the group (Hauser, 1996). Vocalizations were also produced when food has been found, for instance the frequency of calls may be increased when food is close i.e. in a captive situation when the keeper has entered the enclosure and is preparing the food and indeed the acoustics of these vocalizations may vary depending on whether the food is of high value or not (personal observation). Certainly in this study, the frequency of the 'contact call' was high, particular at Zoo D where one individual in particular called for her food when it was feeding time. Growl vocalizations tended to be produced as a threat and thus consequently were produced when the vet walked by or if there was a keeper present who had been involved at some point with veterinary care or catching of individuals within the group. Zoos B and D in particular elicited a higher frequency of these calls in comparison with other zoos and this was probably due to the fact that individuals within the groups had received veterinary treatment on a number of occasions. Also, it is common practice for infants to be caught and micro-chipped, thus if this had happened recently in the group they tended to be more wary of the keepers' movements for example at Zoo E. Squeal vocalizations were sometimes produced by juveniles who were frightened or were 'told off' by a more dominant individual. This was certainly the case for male juveniles in this study population, as many were approaching the age of being more confident and beginning to test their dominance with other members of the group, for example at Zoos B, C and D. Grunt vocalizations were generally produced before, sometimes during and after mating and were most frequent at zoos B and D. These

zoos also exhibited the highest time spent in mating behaviour in comparison with other zoos.

Aggression

Overall, Zoo B elicited the highest frequency of aggression, but this was still at a very low level. It has been found that lion-tailed macaques have a rich repertoire of reassurance patterns and a high rate of reconciliation, indicating that this species readily re-establishes 'friendly' relationships after an aggressive encounter within the group (Abegg *et al*, 1996). Threat facial displays are also used as part of aggression and once again this was exhibited at very low frequencies, but mostly at Zoos C and D. Appeasement facial displays are a sign of affiliation and thus are often used in reconciliation after an aggressive encounter (Abegg *et al*, 1996). This was exhibited at similar frequencies to aggression and was most frequent at Zoo B, thus once again indicating that this is a highly reconcilable species. It has also been found in another species of macaque, the tonkean macaque (*Macaca tonkeana*), that behaviours such as lipsmacking, clasping, mounting and social play, were mainly used to successfully halt aggression (Petit & Thierry, 1994). Indeed, in the present study the frequency of mounting was very low and many occurrences were used to re-establish dominance.

Abnormal behaviours

As already mentioned, the 'hand-to-eye' behaviour was only exhibited by three individuals. All were females and interestingly these females were the older individuals of the group. It was initially thought that this was an abnormal behaviour (Wijgergangs, 1993), however, from observations in this study it appears that this is not the case. This behaviour was normally performed when individuals were waiting for food and thus were sitting in a set position looking for the keeper, or when they were searching for food from above. Thus, it is thought that this behaviour in some way helps the individual focus on objects at a distance, but obviously further research would need to be considered to confirm this hypothesis.

Differences between adult and juveniles

It has been stated that, "Adolescence, the period between puberty and the attainment of full adult size appearance, is a distinct and important developmental period in primates" (Setchell, 2003). Thus, when analysing the behavioural development in male mandrills (*Mandrillus sphinx*), Setchell (2003) found that as age and morphological development increased, social behaviours (grooming and play) decreased, involvement in aggression increased, and sexual behaviour increased per time that males spent with the social group. In part, this correlates with what was observed in this study. Data was not analysed or separated between males and females therefore comparisons were not made. Adults showed greater rates of allogrooming and resting but spent less time involved in social interactions such as play. It was observed that aggression was mostly between adults or between an adult and a juvenile, in which the adult was normally re-establishing its dominance over the juvenile.

Effect of time of day on behaviour

As already stated, time of day only seemed to significantly influence feeding behaviour in the captive population of lion-tailed macaques. Feeding was at its highest during the afternoon (15:00h – 17:00h) across all zoos, as this was the time when the macaques received their main fruit feed.

In wild populations of another macaque species, the Buton macaque (*Macaca ochreata brunnescens*), one of the significant differences found was that time spent resting was significantly lower in the early morning (06:00 – 10:00) than during the remainder of the day (Irving-Lewis, 2003). There are also temperature and thus weather influences in the wild to consider, whereas captive animals are affected by routine. In protected forests, lion-tailed macaques' resting time decreased during months of relatively low food availability, as they were having to forage for longer to find adequate resources (Menon & Poirier, 1996). Perhaps the mean time spent

resting for each of the groups in the present study would be higher if observations started at sunrise as observed in wild studies.

Conclusion

Behaviour can be influenced by many external factors, not only in the wild but also in a captive environment and possible effects of such factors will be discussed in Chapter 5. However, from this study on activity budgets it has been found that

- It is possible that captive populations could be used as models for wild fragmented populations, but more groups need to be assessed and compared in order to make it a viable comparison.
- Future work needs to be carried out regarding the nutritional of diets provided by different zoos, possibly through faecal analysis, where comparisons are made between groups. The main focus could be on supplements that are given, and the foraging substrate provided, to see if any relationships could be found regarding the reproductive success of this species.

Thus, the information gained from the assessment and analysis of activity budgets in a captive environment, may be useful and could become a model for wild populations. The results from this study suggests that fragmentation may alter the activity budgets of wild lion-tailed macaques occupying these fragmented regions of rainforest and thus provides useful information regarding possible implications and consequences for wild populations to a changing habitat.

CHAPTER 5: ENVIRONMENTAL INFLUENCES

Abstract

Many studies have shown that enclosure design, enclosure complexity, feeding enrichment and the presence of visitors, affect the behaviour of captive animals. The aim of this study was to assess how the behaviour of captive lion-tailed macaques was influenced by four factors; enclosure design, enclosure complexity, type of feeding regime and the presence of visitors. This was related to the welfare of captive lion-tailed macaques. At five zoos, the enclosure size, enclosure complexity, type of feeding regime and the number of visitors were ranked on a scale from one to five, with one being the smallest, least complex, most routine type of feeding and the least number of visitors and vice versa for rank five. Behaviour data from Chapter 4 was categorised into active, inactive, food related and social behaviours. Correlations were then carried out between these behaviours and the environmental factors. Only three correlations between environmental factors and behaviour were significant. Enclosure size was found to significantly influence the time spent on active behaviours by, as the enclosure size increased, the time spent performing active behaviours decreased during the morning sampling period. In addition, enclosure size was also found to influence the time spent performing inactive behaviours during the afternoon sampling period, where by as the enclosure size increased, the time spent performing inactive behaviours decreased. Also during the afternoon sampling period, it was found that as the enclosure complexity increased, the time spent performing active behaviours also increased. The type of feeding regime and the effects of visitors had no significant effect on the behaviour of captive lion-tailed macaques. This study highlighted that the lion-tailed macaque benefits from a complex environment with structural and feeding enrichment acting as a key to stimulating natural behaviours. Therefore, several factors can influence the behaviour and welfare of captive lion-tailed macaques, which may have an impact on their breeding success. As this species is becoming increasingly endangered it is increasingly important to have appropriate captive environment.

Recently, zoos have progressed from old, traditional enclosures to naturalistic "habitats" however decisions on enrichment are often based on visitor experience as well as animal-related issues. Thus, enclosures are often designed to increase animal visibility as well as to decrease abnormal behaviours, and stimulate natural behaviours in a natural pattern. There is no set definition for natural behaviour, therefore many questions are posed, such as when captive animals are given more space or allowed outdoors, is their behaviour adapted to the habitat or is it from when their predecessors were caught (Newberry, 1995)? In this chapter, 'natural behaviour' will be defined as the species typical behaviour that is exhibited by both captive and wild lion-tailed macaques.

In the 1980s, zoos orientated much of their long-term propagation programmes toward the idea of eventual reintroduction of animals to nature. However in a many cases these reintroduction processes may not occur for at least 100 years due the problems of establishing suitable habitats with the correct available resources. Therefore, the idea of wildlife conservation parks and zoos becoming "environmental resource centres" has recently come to light (Koontz, 1997). For animals in genetic conservation programs, the future survival and reproductive success of animals should be enhanced by providing the animals with opportunities to learn the characteristics of natural food items and predators at appropriate stages of development, and to develop flexibility in behaviour in order to adapt to a changing environment. Thus, enrichment should result from modifications to the captive environment to make it more similar to that of the environment where it is intended that these animals will be released (Newberry, 1995).

In several primate studies it has been found that after moving captive primates to naturalistic exhibits, individuals have been observed to increase species-typical activity, including locomotion, feeding and object examination (Chang *et al*, 1999). However, there have been reports of a decrease in social behaviour and aggression, perhaps as a result of the increase in private spaces that comes with larger, more

complex exhibits (Lukas *et al*, 2003). Lukas *et al* (2003) also stated that in addition to changing exhibit structure and appearance, improving the naturalistic qualities of a captive environment may involve the provision of browse or other manipulable materials, and although zoos do regularly implement stimulus change and exposure to novelty as critical elements of behavioural enrichment, a distinction should be made between absolute and relative novelty. Absolute novelty refers to stimuli that contain some qualities that have never been experienced, and relative novelty results from familiar stimulus elements combined in a different way.

Therefore changes to an animal's environment such as increasing the enclosure size, adding enrichment thus making the enclosure more complex, altering the feeding regimes by providing a varied diet and distributing food in a number of ways are all likely to influence an animal's behaviour. Margulis *et al* (2003) stated that "zoo visitors have been variously characterised as being enriching for zoo animals, as being stressors, and generally influencing behaviour in measurable ways" therefore, it is important to also take into account how visitors influence an animal's behaviour when regarding the welfare of that species.

5.1.1. Aims

The aim of this study was to assess how the behaviour of captive lion-tailed macaques is influenced by four main environmental factors: enclosure design, enclosure complexity, type of feeding regime and the presence of visitors. This was related to the welfare of captive lion-tailed macaques.

5.2. Methods

Enclosure size

For each zoo, enclosure size was estimated using the enclosure plans that had been drawn for Chapter 3. The five zoos were then ranked an enclosure size from one to five, with one representing the zoo with the overall smallest enclosure (both indoor and outdoor) and five representing the zoo with the overall largest enclosure (both indoor and outdoor) (see Table 5.1. and Appendix 5, plates 1 and 2).

Enclosure complexity

In regards to enrichment, enclosure complexity was assessed by describing the physical structures within the enclosure, if any foraging material was provided, the differences in size between the indoor and outdoor enclosures and if the enclosure in general provided a complex environment, which encouraged the lion-tailed macaques to perform variety of different behaviours. The five zoos were then ranked from one to five with one representing the zoo with the most barren enclosure with least enrichment and five representing the zoo with the most complex enclosure, with the largest indoor and outdoor enclosures and the most enrichment (see Table 5.1. and Appendix 5, plates 3 and 4).

Feeding regimes

From the surveys (see Chapter 2) and throughout observations, feeding regimes were noted, such as the time of day the animals were fed, how they were fed (i.e. scatter fed, fed indoors or outdoors etc) and the type of food provided. In particular, any additional or novelty food items given were noted as this indicated good variation in the macaques' diet (see Table 2.2, Chapter 2). The five zoos were then ranked from one to five with one representing the zoo with the most routine type of feeding regime with little variation and five representing the zoo with the most varied feeding times and overall regime (see Table 5.1. and Appendix 5, plates 5 and 6).

Throughout behavioural observations (see Chapter 4) the number of visitors was recorded. This was done by scanning round the enclosure at the beginning of the behavioural observations and recording the number of visitors surrounding the enclosure. This was increased accordingly as more visitors arrived. When there was a large crowd of visitors, for example, a school group, an estimation of the number of individuals within the group was made. The number of visitors was then averaged over the 12 days for each zoo. The five zoos were then ranked from one to five with one representing the zoo that had the lowest average number of visitors and five representing the zoo that had the largest average number of visitors (see Table 5.1.).

5.2.1 Descriptive and statistical analysis:

Using the mean time spent performing state behaviours (%) at each zoo (see Chapter 4, 4.3.1), the most common behaviours were categorized into four classes (see Table 5.2.).

The data were tested for normality using the one-sample Kolmogorov-Smirnov test in SPSS (version 12.0) and Pearsons correlations were performed between all behaviour classes and environmental factors for each zoo and for each sampling period. Graphs were then plotted representing any significant correlations found between behaviour and environmental factor.

Table. 5.1. Zoos ranked from lowest or worst (rank 1) to highest or best (rank 5) in relation to four environmental factors

Environmental factor and rank	**Zoo**	**Description of zoo**
ENCLOSURE SIZE		
1	B	Overall small enclosure, limited space for the number of individuals held within the group.
2	D	Medium enclosure size in between 1 and 5.
3	E	
4	C	
5	A	Overall very large enclosure.
ENCLOSURE COMPLEXITY		
1	B	Bare floors inside, woodwool for foraging and bare cage outside with straw for foraging, little enrichment.
2	E	Good foraging material outside, very basic indoor enclosure. Little enrichment.
3	A	Very large outdoor enclosure with good foraging material of grass and lots of climbing apparatus.
4	D	Good sized enclosure both indoor and outdoor. Foraging material of straw and grass. Good enrichment.
5	C	Excellent sized indoor and outdoor enclosure. Lots of enrichment and foraging material of grass and bark.
FEEDING REGIMES		
1	E	Fed main meal same time every day, food always placed in same spot, little variation in diet.
2	A	Fed main meal same time of day, scatter fed, a little variation in diet.
3	B	Fed main meal same time of day, scatter fed. Foraging food provided. Some variation in diet.
4	C	Feeding time varied, scatter fed. Foraging food provided, including browse. Good variation in diet, location of main food varied (alternated between indoor and outdoor).
5	D	Feeding time varies, scatter fed, food placed in novel objects. Foraging food provided. Good variation in diet, location of food varied (indoor/outdoor).
VISITOR NUMBERS		
1	E	<20 per day. Low number of average visitors, few visitor-animal interactions.
2	D	20 – 50 per day
3	A	50 – 100 per day
4	B	100 – 200 per day
5	C	200 – 300 per day. High number of average visitors per day, frequent animal-visitor interactions per day.

Although there were other behaviours listed under these categories in the ethogram, (see Table 2.3, Chapter 2), it was thought that the behaviours listed in Table 5.2 would be most influenced by environmental factors (Newberry, 1995) and these were also the most common behaviours exhibited by all of the groups.

Table 5.2. Categories of behaviour

Category	**Behaviour**
ACTIVE	Locomotion
INACTIVE	Resting
FOOD RELATED	Foraging and feeding
SOCIAL	Social play, mating and allogrooming.

Only three correlations between environmental factors and behaviour were significant. The mean time spent performing active behaviours was found, to be influenced by enclosure size and enclosure complexity, and the mean time spent performing inactive behaviours was found to be influenced by enclosure size (see below).

Enclosure size

09:00h – 11:00h

Enclosure size was found to significantly influence the mean time spent performing active behaviours (Pearsons correlation, N = 5, r = -0.993, p = 0.001) during 09:00h – 11:00h (see Figure 5.1).

Figure 5.1. The effect of enclosure size on the mean time spent performing active behaviours from 09:00h – 11:00h.

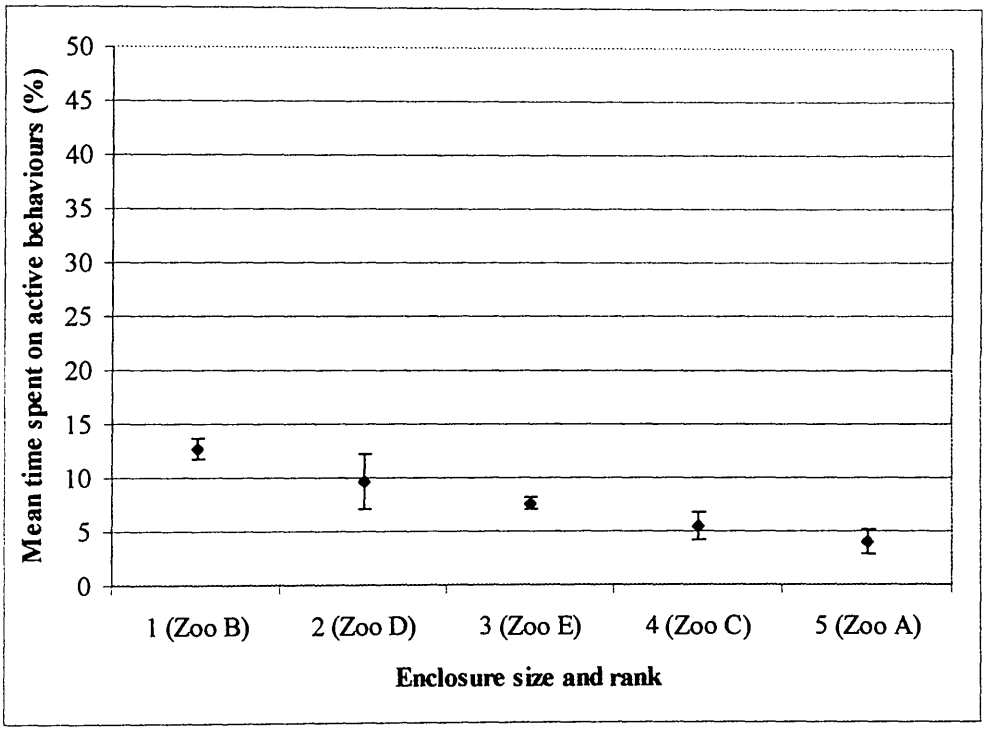


Figure 5.1 showed that as enclosure size increased, the time spent performing active behaviours, i.e. locomotion decreased. Zoo A exhibited the lowest mean percentage of time on locomotion, but had the largest enclosure. By contrast, Zoo B animals, exhibited the highest mean time spent on locomotion, but had the smallest enclosure.

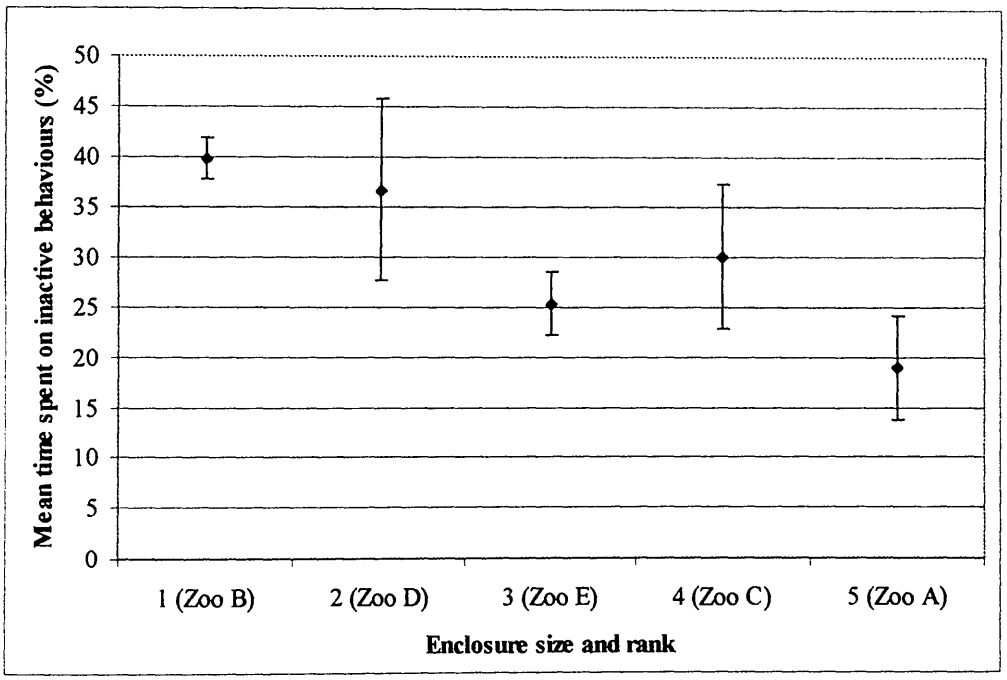
12:00h – 14:00h

No significant correlations were found during this sampling period.

15:00 – 17:00h

In the afternoon sampling period (15:00h – 17:00h) enclosure size significantly influenced the mean time spent performing inactive behaviours i.e. resting (Pearsons correlation, N = 5, r = -0.920, p = 0.027) (see Figure 5.2.). As the enclosure size increased the mean time spent performing inactive behaviours significantly decreased.

Figure 5.2. The effect of enclosure size on the mean time spent performing inactive behaviours from 15:00h –17:00h.



Thus Zoo B had the smallest enclosure and was the most inactive. In contrast Zoo A had the largest enclosure and spent the least time on inactive behaviours.
No other significant correlations were found between enclosure size and behaviour.

Enclosure complexity

09:00h – 11:00h

No significant correlations were found during this sampling period.

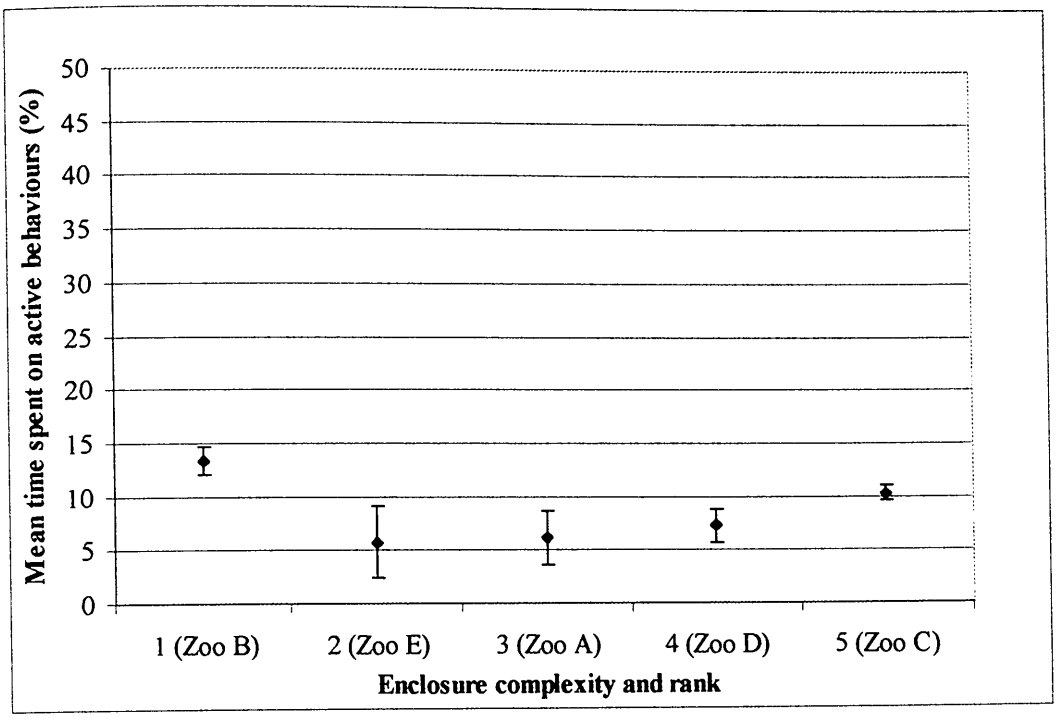
12:00h – 14:00h

No significant correlations were found during this sampling period.

15:00h – 14:00h

When assessing the influence of enclosure complexity on behaviour, a significant correlation was found between this factor and the mean time spent performing active behaviours (Pearsons correlation, $N = 5$, $r = -0.952$, $p = 0.013$) between 15:00h – 17:00h (see Figure 5.3). As the complexity of the enclosure increased, the mean time spent performing active behaviours also increased. Therefore, zoos with lots of enrichment such as Zoo C encouraged the lion-tailed macaques to be more active compared with Zoo E, which does not implement much enrichment animals there showed a low level of active behaviours. Zoo B, however, was ranked the lowest in enrichment, but this group spent the highest proportion of time in active behaviours in comparison with the other zoos.

Figure 5.3. The effect of varying enclosure complexity on the mean time spent performing active behaviours from 15:00h – 17:00h.



No further significant correlations were found between enclosure complexity and any other behaviour for any of the sampling periods.

Feeding regimes

No significant correlations were found between feeding regimes and any of the behavioural categories, for any of the three sampling periods.

Visitor effects

No significant correlations were found between visitor numbers and any of the behavioural categories, for any of the three sampling periods.

Carlstead and Shepherdson (1994) stated that, "captivity imposes on animals that are naturally from the wild, an environment that differs vastly from that in which they have evolved. To thrive in captivity, a species must accommodate these differences. The ability of a species to respond to captive conditions with behaviour from its normal repertoire, depends on the degree to which the particular captive condition resembles its natural environment". Indeed, the behavioural repertoire of captive lion-tailed macaques indicates that this species, in the majority of cases, exhibits its 'normal' behaviour and thus has an ability to accommodate the differences that it faces in captivity (see Chapter 4), particularly as no 'abnormal' behaviours were observed. However, what is clear from this study is that the overall activity budgets of lion-tailed macaques are influenced by captivity, but more from their surroundings through enclosure size and complexity than through external and unnatural factors such as the effects of visitors or the way their food is distributed.

Zoos are selective about the types of "natural behaviours" that are considered acceptable, both from an animal husbandry viewpoint as well as with respect to the publics' reactions (Little & Sommer, 2002). In Little's and Sommers (2002) study on Hanuman langurs (*Presbytis entellus*), they stated that langurs in the wild experience predation, infanticide by incoming males, high infant mortality, increased aggression due to spatial proximity around clumped food sources, and fierce male-male competition for females, including mutual killings. However, zoos will try to minimize the occurrence of such natural events to avoid scenes that visitors may find disturbing. They are therefore defeating the very goal of inducing "species-typical levels of behaviour". Of course if zoos were not selective, the welfare of that captive species would be impaired and with current legislation and through visitor complaints, any zoo allowing behaviours such as those in wild langurs to be exhibited, it is likely that the zoo would be unable to house that species and possibly any species again.

A larger enclosure size does appear to decrease the time spent on locomotion by lion-tailed macaques, which at first seems unusual, as it would be predicted that if an animal had more space, it would spend a higher proportion of its time moving around the enclosure. As already stated, Zoo A had the largest enclosure, but the group spent the lowest proportion of time on locomotion in comparison with other zoos. One possible reason for this is that the exhibits with larger enclosures tended to contain more foraging substrate such as grass. Indeed, Zoo B showed the highest rate of locomotion, but had limited foraging material within its enclosure. Thus, exhibits with larger enclosures and vast foraging material appear to decrease the time spent on general locomotion, which influences when animals are either waiting to be fed or are suffering from boredom. The opposite effect was found regarding the influence of enclosure size on the mean time spent performing inactive behaviours where, as the enclosure size increased, the mean time spent resting decreased as animals were actively foraging in the larger, more enriched enclosures.

Observations of changes in behaviour in relation to enclosure size have been observed in gorillas and langurs. Lukas *et al* (2003) monitored the behavioural differences of groups of gorillas when housed in a small enclosure compared to when they were moved to a larger enclosure, and found that in the smaller exhibit, gorillas engaged in more undesirable behaviour, such as self-directed behaviour and reclining. They decreased social contact, increased social distance, increased the use of grass areas within the exhibit, and decreased the use of small concrete areas adjacent to the holding facility. In a study on captive langurs, there was a concern that this primate was in poor physical condition through lack of exercise, predominantly from being housed in a small enclosure, thus it was moved to a new larger enclosure (Little & Sommer, 2002). The benefits of this were immediately noticeable as the langur was performing leaps of up to six metres soon after being introduced into the enclosure. There was a reduction in aggression, probably as a result of the opportunity to disperse.

Some zoos in this study on lion-tailed macaques showed a daily alteration between indoor and outdoor exhibits and it was often common practice to shut animals out in their outdoor enclosure for the whole day. This gave the keepers a chance to clean the indoor exhibits, but this procedure was mainly done for the benefit of the visitors, so that the animals could be observed at all times. Zoos A, D and E all followed this procedure unless the weather was extremely adverse, where keepers would then allow access between the two enclosures. Interestingly, in some primates there seems to be a correlation between this change of enclosure and behaviour. In gorillas, it was found that exhibit use, generalized activity and social approaches increased during the novel phase of introduction into the second enclosure. The gorillas' use of grass areas in the exhibit and the amount of time the gorillas were visible to zoo visitors increased significantly during the 4 day introduction to a second enclosure. The same has been observed in small nocturnal primates (*Galago*) (Lukas *et al*, 2003). Perhaps this method increases the welfare of captive primates, as although the enclosure will be the same from day to day it does stimulate the animals to explore, and consequently perform behaviours that might not be exhibited if these animals were housed in the same enclosure every day.

Therefore, by placing primates in a larger enclosure and alternating animals between two enclosures, the extra space and novelty of a different enclosure can encourage individuals to become more active and consequently perform more species typical behaviours. Enclosure complexity is likely to strongly coincide with this, as in general, in a larger enclosure the environment tends to be more enriched, and thus contains substrate or equipment that encourages more 'natural' behaviours. This has been seen with the lion-tailed macaques where as already stated, this species is more active in larger enclosures and as most zoos in this study alternated the lion-tailed macaques between enclosures, this encouraged them to explore their new enclosure each day.

When comparing the behaviour of a species housed in a barren exhibit to the behaviour it exhibits in a structurally enriched exhibit, behavioural changes have been observed. One example of this is when the behaviour of Indian Leopards (*Panthera pardus*) was compared between four zoos in Southern India (Mallapur *et al*, 2002). In this study it was found that the activity levels of the leopards were significantly higher in the structurally enriched environment and thus the complex environment stimulated the exhibition of natural behavioural repertoires. This certainly correlates with what was observed in the present study, when assessing the effects of enclosure complexity on the lion-tailed macaques behaviour. Zoos with much enrichment such as ropes and platforms, for example, Zoo C encouraged the lion-tailed macaques to be more active. As the enclosure complexity increased, the mean time spent performing active behaviours increased with one exception. Zoo B showed the highest mean time spent performing active behaviours in comparison with the other zoos, however this was in the least enriched environment. A possible explanation for this observed difference is that individuals within the group at Zoo B were often observed pacing between the indoor and outdoor enclosures in anticipation of feeding times and thus watching for keepers. As previously stated, little foraging material was provided in this enclosure, therefore more of the macaques' time was spent moving around the enclosure in comparison with the other zoos. Providing physical enrichment, such as foraging material and feeding devices, strongly influences the behaviour of captive animals and this will be discussed later on in this chapter.

The structural environment surrounding captive animals also adds to the complexity of an enclosure and this along with physical enrichment seems to be the key to promoting the welfare of captive species and even the smallest change in environment can have a big impact. Space can be increased, by adding an upper tier or vertical partitions to divide internal space into different functional areas. Walls can also be made more inhabitable for some species by providing ledges and climbing holes. An animal may gain a feeling of security if provided with opportunities for

camouflage and hiding (Newberry, 1995). Zoo C was shown to have all these features and as already stated this group was most complex and showed the highest activity. Another example of where the physical structure of an enclosure has been changed is the use of vertical space to improve the welfare of orangutans (Herbert & Bard, 2000). It is well documented that these primates are arboreal and thus favour habitats in trees. In captivity it is often hard to create a forest canopy that would match an orangutan's natural habitat. Thus, Herbert & Bard (2000) monitored how orangutans used an innovative zoo habitat that contained a flooded floor, retractable skylights, four moulded trees and interwoven vines. They found that the orangutans favoured the upper canopy, which contained many tree limbs for sitting and reclining. The orangutans next favoured the lower canopy and the skylights above the upper canopy, especially those skylights that were out of public view. The exhibit designer's method of flooding the floor was effective as the orangutans avoided this and thus the exhibit highlighted that even in captivity this was an arboreal species. Chang *et al* (1999) analysed the behaviour of a confined group of mandrills (*Mandrillus sphinx*) when they were housed in a traditional enclosure and then when they were relocated to an "ecologically representative" exhibit (Chang *et al*, 1999). They found that the time spent foraging, feeding and on locomotion increased and the time spent resting decreased. However, they found a decrease in some social behaviour. It was suggested that these differences in behaviour may have been due to changes in the "proximate environmental contingencies" such as more feeding and foraging opportunities in the new enclosure, increased social refuges, a slight increase in enclosure size and a significant increase in environmental complexity and novelty. This study once again, highlights, that primate welfare is not purely influenced by the extent of the confinement, such as the enclosure size, but also by the presence of relevant incentives to engage in species-appropriate behaviour.

In conclusion, the above studies on orangutans and mandrills highlighted that species appropriate habitats have a beneficial effect on the welfare of captive animals by providing opportunities for a range of species-typical behaviours. This study is an excellent example of how the enclosure complexity can be modified to a species'

requirements, and in this case improve the welfare of a shy, arboreal primate, which, with these characteristics, is very similar to the lion-tailed macaque.

Feeding regimes

Captive primates are usually provided with a more limited selection of food types than those available in natural habitats. Offering a wide selection of food types can be a good source of enrichment, especially for species with generalist diets. Also, greater food variety and the way it is distributed stimulates foraging and feeding behaviour, thus improving the physical condition of an animal by keeping it active and possibly improving its nutrition to match that of its wild counterparts (Newberry, 1995). Although in the present study the type of feeding regime had no significant influence on the lion-tailed macaques' behaviour, from observations it was apparent that the level of nutrition of lion-tailed macaques varied between zoos, as already suggested as the possible reason for the observed differences in mean time spent feeding and foraging between zoos (see Chapter 4). Included in the diet of captive lion-tailed macaques were unfavourable items such as chewing gum, sweets, crisps and so on provided by visitors, and how visitors influence lion-tailed macaque behaviour will be discussed later on in this chapter.

The aim of feeding enrichment is improve the welfare of captive animals and it also adds to the experience of the zoo visitor (Bashaw *et al*, 2003). Bashaw *et al's* (2003) study on feeding enrichment in captive large felids, e.g. lions (*Panthera leo*), found that the presentation of live fish increased the variety and frequency of feeding behaviours, while presentation of horse leg bones increased only the frequency of feeding behaviours. Both types of food enrichment were found to reduce stereotypic behaviour. In spectacled bears (*Tremarctos ornatus*), feeding enrichment was found to significantly extend the time bears spent foraging (Fischbacher & Schmid, 2000). Feeding devices such as jug foraging puzzles, have also been shown to influence the behaviour of single-cage rhesus macaques (Schapiro *et al*, 1995). It was found that the macaques spent significantly more time feeding when enrichment foods were provided, but also more time was spent playing and using enrichment devices when

they were available, thus the suggestion was made that devices may be more valuable than foods. Therefore, Schapiro *et al* (1995) concluded that feeding enrichment programmes that combine stimulating devices with foods that are novel and require processing can positively affect the behaviour of captive primates. Also, as seen in this study on lion-tailed macaques, providing grass or bark foraging substrate instead of woodwool and straw does seem to increase the time spent foraging (see Chapter 4).

Feeding enrichment does encourage natural behaviour of captive animals, but the success of such enrichment programmes needs to take into account the feeding habits and learning ability of individuals at different ages, and the influence of social dynamics on access to food (Newberry, 1995)

Visitor effects

As previously stated, visitors can have a positive and negative effect on an animal's behaviour. In this study, the number of visitors did not significantly influence the lion-tailed macaques' behaviour. This was surprising, as during this study many of the young macaques, particularly juvenile males, were observed to be attracted to the window when visitors were present. This was particularly true when children were present, as in most cases the children were holding food or brightly coloured toys. School children often teased the animals and the macaques sometimes responded by intentionally bounding off the windows. Unfortunately this behaviour actually encouraged the children to persist in banging on the window. As already mentioned, the macaques did receive food from the public, particularly at Zoos A and B. Therefore, as expected, when visitors with food were at the enclosures of these two zoos the macaques would often try and grab food from the visitors. This did not occur at Zoos C, D and E due to the enclosure design (see Chapter 2), as the indoor enclosures had glass viewing windows, and the outdoor enclosures consisted of islands. The visitors therefore could not have physical contact with the macaques. It is unknown whether these additional artificial foods have any effect on lion-tailed macaques, however, it has been documented that in free-ranging Barbary macaques

(*Macaca sylvanus*) in Gibralter consuming high calorific foods from tourists and having readily available access to natural foods is causing weight problems in these macaques and thus the health and welfare of this population is being affected (O'Leary, 1996).

In a study comparing the influence of visitors on 12 different species of primates, behaviour did seem to be affected (Hosey & Druck, 1987). Hosey and Druck (1987) found that the presence of the public appeared to have no significant effect overall on the frequency of interactions between primates in the same group. However, locomotory activity was significantly increased and there was an indication that animals spent more time at the front of the cage when a large active audience was present. Thus, they concluded that zoo primates do not habituate completely to the presence of the public, but nor do they ignore them. Indeed, in many cases, particularly in the larger enclosures, such as at Zoos A and C, the lion-tailed macaques did often ignore the public and continued with their activity. All zoo enclosures had at least one area where the lion-tailed macaques could escape from visitors. It was also found that enclosures that had elevated platforms appeared beneficial regarding visitor interactions, as the macaques would often rest on these platforms and visitors would pass by these enclosures and never looked up, thus thinking that the enclosure was empty. This meant that the lion-tailed macaques remained undisturbed however it possibly means that there is a decrease in the education received by the public regarding this species. This was observed frequently when the macaques at Zoo C were in their indoor enclosure and when the macaques at Zoo B were in their outdoor enclosure.

Thus, it can be seen that visitors do seem to influence the behaviour of captive primates, thus in some enclosures camouflage netting is now being put up as a visual barrier between primates and visitors. When a camouflage net was placed in the viewing area of one gorilla exhibit it was found that the gorillas exhibited significantly lower levels of conspecific-directed aggression and stereotypic behaviours (Blaney & Wells, 2004). From a visitors' perception the gorillas were said to look more exciting and less aggressive. Thus this introduction of netting had a

positive effect, as it resulted in the reduction in behaviours that are typically induced by large groups of visitors, such as aggression and it also improved the public perceptions of the animals and their environment. A similar screening barrier was observed at Zoo C during the present study as one-way windows had been incorporated into the orangutan enclosure so that visitors could observe the orangutans, but the orangutans could not see the visitors. These methods of have been shown to have a positive impact on the welfare of captive primates and more studies such as this are being developed.

In a survey of visitor perception of enrichment, it was found that visitors felt that natural objects within the enclosure made "the animal feel more at home" and that non-natural objects were often associated with activity, thus the visitors felt that these objects were there for the animal to "play with" and "to keep the animal from getting bored"(McPhee *et al*, 1998). Unfortunately, enrichment decisions still often focus less on animal needs and more on visitor needs. However, zoos are beginning to focus on educating the public and indeed from carrying out observations for this study on lion-tailed macaques it was clear that a greater effort is being placed on providing information regarding a particular species next to their enclosure. Some zoos are also putting information boards up stating what types of enrichment they place in enclosures, why the enrichment is carried out and how it is implemented. Some zoos are better at incorporating this educational message across to the public than others, but hopefully over the next few years all zoos will be setting the same standard.

Conclusion

This chapter has highlighted that certain environmental factors influence the behaviour of captive animals, thus affecting the welfare of that species. However recommendations are continuously being made and solutions are being found on ways to improve captive conditions and thus the welfare of zoo animals. Many studies have assessed the effects of changing an animal's enclosure on its behaviour as already stated.

This study and others have shown that primates,

- benefit from a complex environment with structural and feeding enrichment acting as a key to stimulating natural behaviours.

- Although visitors appeared not to influence the lion-tailed macaques' behaviour significantly, they do affect their diet by hand feeding the macaques and appropriate measures should be taken so that no physical contact can occur between the macaques and the visitors.

Zoos are now coming into an era where one of their primary aims is to educate the public of the animals that are left in the wild and, through the use of environmental enrichment, convince the protesters against zoos that their establishments are running for educative reasons and in some cases are protecting the remaining population of a species that is on the brink of extinction. Through environmental enrichment, a zoos prerogative is to maintain the welfare of captive species and as seen in this chapter a lack of abnormal behaviours in the captive British and Irish lion-tailed macaque population indicates that the welfare of this species is good, especially in comparison to behaviours of this species observed in Indian zoos (Mallapur pers.com).

Therefore, several factors can influence the behaviour and welfare of captive lion-tailed macaques and possibly their breeding success. As this species is becoming increasingly endangered it is increasingly important to have appropriate captive environment.

CHAPTER 6: GENERAL DISCUSSION

The lion-tailed macaque is one of the most endangered species of primates, with less than 2500 individuals inhabiting the tropical rainforests of the Western Ghats, India (IUCN, 2003). This rare species is shy and less vocal than most primates, they are one of the least studied (Easa *et al*, 1996). In the wild, many populations are now becoming isolated due to habitat fragmentation and in captivity the population has high infant mortality, a low number of births that fluctuates from year to year and a significant proportion of adult females not breeding (Krebs & Kaumanns, 2002). Consequently, both in captivity and in the wild there is a risk of this species losing its genetic diversity, which has strong implications for this species' ability to adapt to and survive in a changing environment. Therefore, the aims of this study were to assess the social structure, spatial relationships and activity budgets, including environmental influences on behaviour, in the British and Irish captive population of lion-tailed macaques and to relate the findings to the reproductive success of captive populations and also to what has been observed in wild fragmented populations. Thus, the overall aim was to discuss the implications of possible reintroduction programmes of lion-tailed macaques and suggest ways of sustaining the captive population as a viable resource for these reintroduction programmes.

The effects of captivity on lion-tailed macaques

The behaviour and use of space by animals both in the wild and in captivity are substantially restrained by their surroundings (Lukas *et al*, 2003). In wild fragmented populations, animals have limited space, a limitation in available resources such as food, and possibly if the group is isolated, a reduction in genetic diversity due to the lack of immigration and emigration of individuals. Animals in captivity also face these restrictions and have the added problem that they have most likely been born in captivity and consequently may have developed a different behavioural repertoire compared to their wild counterparts. A number of reintroduction programmes have indicated that many of the deaths of reintroduced animals are due to behavioural deficiencies, such as the inability to utilise available resources (McPhee, 2003).

Thus, it is important that species in captivity if possible, are exposed to stimuli that are similar to those they will experience in their natural environment.

As many species are experiencing habitat fragmentation, it is also necessary to study the behaviour of species in captivity to monitor behaviour in a restricted habitat and state possible implications on behaviour for wild species that are facing similar habitat restrictions. Enclosure design, the size of the enclosure, its complexity as well as the social opportunities are likely to impact upon captive lion-tailed macaques behavioural development.

Social structure and spatial relationships

In the current study on captive lion-tailed macaques in British and Irish zoos, the social structure differed between zoos and differed in comparison to the wild population, with group size being much smaller in captivity. Zoos do not have sufficient space to house large groups of lion-tailed macaques in captivity, thus often when a group is becoming too large individuals have to be moved to another institution. Consequently, the social structure of groups in captivity is affected, as many groups consist of both related and unrelated individuals. In the current study, the presence of related and unrelated individuals appeared to affect the spatial separation distances between individuals, with related females being in much closer proximity to the dominant female and to each other than unrelated individuals.

It has been suggested that the presence or absence of unrelated individuals may influence the degree to which macaque mothers encourage independence in their infants and tolerate their interaction with others (Berman *et al*, 1997). In free-ranging rhesus macaques it has been found that in general, mothers tend to tolerate interaction with their own close kin and do not tolerate unrelated individuals. When comparing mother-infant interactions with increasing group size, it was found that mothers spent more time near their infants and sought closer proximity to them as the group size expanded, and infants tended to form social networks that were highly focused on close kin in these larger groups (Berman *et al*, 1997). Also as the group

size increases in a small enclosure it is probable that there would be an increase in aggression between individuals due to the fact that individuals will have to be in closer proximity to each other. This was found in this study on lion-tailed macaques where aggression was prevalent at Zoo B. The group had a young infant in the group and aggression was often directed from the mother to juveniles when they were playing. From an early age, it appears that infants learn from their mother which individuals to associate with. Thus, introducing an older individual into a group of related individuals, is likely to have welfare implications for that individual, as it would be an 'out cast' in relation to other members of the group. This is apparent from this study on lion-tailed macaques, that where unrelated individuals have been found to distance themselves from the rest of the group and also be of quite low rank in the dominance hierarchy, access to resources such as food was restricted until dominant individuals had taken advantage of these resources. The implications this has for wild populations is that, if populations become fragmented, unrelated individuals may be forced to join other social groups and due to being place near the bottom of the dominance hierarchy, they will suffer if there are limited resources. Although enclosure size was not found to significantly influence these spatial distances between individuals, it was clear from comparing the spatial maps (see Chapter 3, Figure 3.5) with enclosure size, that there is a tendency for large spatial distances to be in groups with large enclosures, thus perhaps if more groups were included in this study a significant result would have been produced. A significant result may also have been produced if there were no differences in the number of scans performed on each group, thus perhaps if the same number of scans were performed and more frequently, then this would give a better representation of spatial relationships between individuals.

Ecological variables, such as predation risk and resource availability and distribution are likely to play a major role in a species life history through their effects on spatial relationships, demography and patterns of competition (Berman *et al*, 1997). Food availability, habitat availability and resource dispersion have been suggested as major factors contributing to intraspecific variation in reproductive strategy and group structure in canids (Kamler *et al*, 2004). Among primate species, several

factors have been suggested to affect social organization, including food distribution, risk of infanticide, conspecific competition, habitat dispersion, population density and predation risk (Kamler *et al*, 2004). The same authors found that when studying two wild populations of swift foxes (*Vulpes velox*) the social system and consequently reproduction, was strongly linked to predation, in this case the presence or absence of coyotes (*Canis latrans*). Coyotes spatially displaced swift foxes from their home ranges thus in areas where there were a low number of coyotes, swift foxes adapted a polygynous mating system and consequently increased group size to include nonbreeding females to help increase pup survival. This suggests that if a species has the available space with limited factors such as predation and food resource influencing it, then the group will change its mating strategy and consequently increase its group size due to the extra available resources. In wild lion-tailed macaques, it has been found that they live in distinct social groups with demographic interaction between them consisting only of infrequent migration by males. Parameters of group growth rate and birth rate have been found to be sensitive to group size. Thus, as group size increased and as the number of females consequently increased, the birth rate decreased possibly due to inter-group competition between females and thus competition between resources (Kumar, 1995a). If the wild population is then fragmented, the group size could increase but not much due to the restrictions of the habitat, such as limited resources and therefore, birth rate would be further decreased.

Following habitat fragmentation, where some patches are occupied and others are not, primate groups may become locally extinct from patches that were initially occupied due to factors such as inadequate fragment size, insufficient food resources or shortage of critical food sources (Mbora & Meikle, 2004). When looking at the effects of forest fragmentation on the distribution, abundance and conservation of the Tana River red colobus monkey (*Procolobus rufomitratus*), Mbora and Meikle (2004) found that there were "suitable" unoccupied forests and "unsuitable" occupied forests in the study area. This suggests that the Tana River red colobus may show metapopulation dynamics, i.e. the population is subdivided and patchy in which the population dynamics operates at two levels, within patches and between

patches with local events of colonization and of extinction (Begon *et al*, 1996). Thus, the ability of this species to move between habitat patches may play a key role in determining their distribution within the system. For arboreal primates in particular, fragmentation can be a problem as the intervening matrix between forest fragments can be cultivation and human settlement and many species will not cross these barriers. The lion-tailed macaque is one such species that has been observed to migrate between groups with interconnected forests (Kumar, 1987), however, they have not been observed crossing large gaps between forests separated by cultivation or human habituation (Menon & Poirier, 1996). As this species depends on the immigration and emigration of males in order to maintain its genetic diversity, and also to maintain group size through reproduction, if the dominant male of a group dies and there is no replacement male (i.e. through no immigration or from the absence of male offspring), then the consequences for that group will be fatal. One possible answer to maintain populations in fragmented habitats is to construct interconnecting forests between fragmented areas, enabling individuals to migrate between groups. Captive groups are isolated in a similar way to fragmented natural populations and there is an artificial exchange of males between institutions to maintain this genetic diversity. This appears to mirror the natural situation regarding immigration of males. Although enclosure size in the current study did not significantly influence the spatial relationships between individuals, from the spatial maps, there appears to be a possibility that certainly requires investigation that larger enclosures tends to increase the spatial relationships between individuals. If there is a chance for captive groups to be used for reintroduction programmes, then the ability of captive bred males to disperse in the wild needs to be assessed, along with the ability of a group to make use of all of the available resources within the reintroduced habitat. This is particularly important, as it is likely that the reintroduction area would be much larger than their usual captive surroundings so it would be expected that spatial relationships would be increased in these habitats due to individuals adapting to the additional space over time. Social structure would also conform more to the wild population as with an increase in space and more privacy it would be hope that the reproductive success would increase due to 'mating couples'

being able to gain a distant away from the main group and have no interruptions from visitors, for example.

Reproduction

Wild populations if fragmented are restricted and therefore in some ways they are similar to captive populations, thus it would be predicted that the structure of the dominance hierarchy may be affected and more importantly that the reproductive rate may be negatively affected. In this study it was found that the reproductive success of females varied within and between groups. The age at which females reproduced also varied. In captivity females appeared to reproduce at an earlier age (three or four years) than the wild females, who in general do not give birth until at least six years of age (Kumar, 1995b). This difference in age may explain why the captive population shows a high rate of infant mortality. There also appeared to be a sex bias in infant mortality, where in the study population, 70% of infants were males, 21% were females (8% were unrecorded). This implies that females are the stronger sex at birth, which for a female bonded species is an advantage, however, with a high rate of infant mortality in the captive population, factors causing this need to be assessed.

It was noted that many females had experienced miscarriages, thus this, and the inability of infants to survive once born could be due to nutritional factors, such as the type of food the mother is receiving and if she is ranked low down in the dominance hierarchy there is a possibility that she is not receiving an adequate amount of food. Being in a restricted habitat also means low ranking mothers are unable to gain food from other sources. Nutritional deficiencies have been shown to increase the chance of infant mortality in many species, such as in rabbits (Rommers *et al*, 2004). It was found that feeding level during early gestation in young rabbit does, did not affect the kindling rate (birth rate), total litter size or the number of still born kits (infants), however, a decrease in feeding during the last week of gestation did affect kit survival and birth rate. Zoos do tend to provide female lion-tailed macaques with added nutrition, for example, in the form of baby food, when they are lactating, however, from this study it is clear that groups have varying nutritional

intakes. Some groups had food supplements such as birds, rodents, insects and many plants that were natural to their enclosure and coincidently these groups expressed a more successful birth rate than groups that had not received these extra food sources. Nutrition has also been found to affect reproductive success in L'Hoest monkeys (*Cercopithecus l'hoestia*). A female was found to be producing infants that were too large and thus was unable to give birth. Zoo staff thus decreased the level of protein in her diet and this seemed to correct the problem (O' Sullivan, pers. comm).

It has also been stated that in wild lion-tailed macaque populations, 'mating couples' have been observed at distances of 100-200m from their group (Lindburg & Harvey, 1996). In a captive situation, mating couples cannot achieve this distance from the group due to the restriction of the size of the enclosure. Therefore, couples may often get interrupted either by other individuals within the group, usually unintentionally, such as when juveniles were playing, or by visitors trying to distract their attention. Thus, unsuccessful reproduction could be linked to the nutrition that female lion-tailed macaques receive, but also to mating being interrupted. The chance of a female successfully conceiving therefore decreases. Enclosure complexity has an influence on reproductive success, as enclosures that are more 'natural' have greater feeding opportunities for the macaques, thus increasing the nutritional levels in their diet. In wild populations, individuals have their natural nutritional resources surrounding them, however, if this was depleted through habitat fragmentation, then the diversity of the lion-tailed macaques' diet would possibly decrease and consequently the reproductive success of these fragmented populations may also decrease. Also, if the habitat size was decreased, 'mating couples' would be unable to distance themselves from the group. This is purely speculative at present, but differences seen in this study on captive populations does indicate that future work needs to be carried out, for example, through faecal analysis to ensure that captive lion-tailed macaques are receiving their optimal nutritional diet and whether, if breeding couples were given the space to mate, this would in turn increase the reproductive rate.

As already stated, enclosure size and complexity appears to influence spatial relationships, social structure and the reproductive success of captive lion-tailed macaques. The dominance hierarchy has also been seen to be important in regards to social structure and also influences spatial relationships. Thus, it would be expected that affiliative behaviours such as grooming would be highest in groups with related individuals, where there were shorter separation distances within the group. Indeed, the rate of allogrooming was high in groups with several related individuals and low in groups with mainly unrelated individuals. Consequently, groups with low levels of allogroming exhibited high levels of autogrooming.

Activity budgets of captive lion-tailed macaques' were also influenced by enclosure size and complexity. In this study, the activity budgets of captive lion-tailed macaques appeared to vary between zoos and thus between groups. Larger enclosures influenced the time spent on locomotion, which seemed to be related to foraging. Large enclosures tended to have more foraging material such as grass, and this probably explains why groups spent more time foraging than moving around the enclosure. Foraging, however, can increase aggression among group numbers competing for a limited food resource (Jones & Pillay, 2004). In this study, only a low level of aggression was recorded. This relates to what has been found for wild lion-tailed macaques, suggesting they are a reconcilable species. When aggression did occur it was normally during feeding time, particularly if the group was not scatter fed, thus individuals were competing for the same resource. The only other time aggressive displays were observed in this study was between lion-tailed macaques and other species surrounding the enclosure, such as the Javan langurs (*Trachypithecus auratus*) and the lac alaotra gentle lemur (*Hapalemur griseus alaotrensis*). This indicates that if a group of captive born lion-tailed macaques was reintroduced into the wild, species that were already present within the new habitat need to be considered and thus possible management plans need to be formed (see later in chapter).

The time spent foraging varied between groups and this was due to enclosure layout and foraging substrate. The type of foraging substrate ranged from woodwool and straw, to bark chippings and grass. Grass appeared to elicit the highest rate of foraging in lion-tailed macaques, as it enabled them to have a high intake of invertebrates as part of their diet, thus zoos with enclosures that were predominantly grass meant that a large proportion of the groups activity budget was allocated to foraging. The time spent foraging by one of the groups correlated with what has been observed in wild populations inhabiting protected forests (Menon & Poirier, 1996). The remaining four zoos ranged from enclosures with predominantly grass to no grass and showed a much lower time spent foraging even when compared to wild fragmented populations and this should be taken into consideration when designing enclosures for captive lion-tailed macaques. The mean time spent feeding was similar between zoos and this was the only behaviour that was influenced by time of day. Feeding was highest during the afternoon when all groups were fed, however as already stated regarding reproduction, the nutrition of the groups varied due to the natural abundance of food such as birds, rodents and invertebrates in some enclosures. The frequency of 'coo' vocalizations was also high during this period, as individuals would often call out when waiting for the keepers to feed them. This showed that captive lion-tailed macaques anticipate feeding schedules which has also been reported in stump-tailed macaques (*Macaca arctoides*) where the rates of self-directed behaviour, inactivity, vocalizations and abnormal behaviours significantly increased in times when animals were waiting to be fed (Waitt & Buchanan-Smith, 2001). However, in this study it was also suggested that delaying these feeding times actually made the situation more stressful for these macaques. This is an important factor to consider when forming a group for reintroduction programmes as if animals anticipate feeding schedules then they may be less encouraged to forage for themselves which will obviously have a serious impact on the survivability of the group.

Enclosure size and complexity influences an animals' activity budget and another good example of this is a study on the behaviour of Hanuman langurs (*Presbytis entellus*) to investigate the effects of varying enclosure size and complexity on their

behaviour (Little & Sommer, 2002). When langurs were moved from their old enclosure to a novel naturalistic environment, it was found that they spent more time in solitary behaviours such as feeding, foraging and locomotion and less time in stationary or social behaviours (resting and allogrooming) in the new enclosure. Once again, this correlated with what had been observed in the present study, where in large enclosures with grass foraging substrate, lion-tailed macaques tended to forage individually and spent less time resting in large, complex enclosures.

Overall, captive populations of lion-tailed macaques have been found to rest more than their wild counterparts, although some groups spent similar time spent resting as groups in wild protected forests (Menon & Poirier, 1996). This is possibly due to the fact that in captivity, individuals are not threatened by predation, they have the sufficient food available to them, and thus do not need to travel long distances to find their food. In a fragmented habitat, food is not in constant supply and due to a restricted home range individuals will have to spend more time searching for food in this enclosure, and may have problems obtaining a diverse daily diet due to seasonality in some foods. However, although there is a reduction in food abundance in fragmented populations, due to less area and lower tree density, the vegetation that immediately surrounds the fragmented area tends to consist of coffee plantations and orchards of Mangos, Jack fruits and Guava in which lion-tailed macaques have been observed feeding on (Umapathy & Kumar, 2000).

It has also been observed that wild groups of lion-tailed macaques in fragmented areas play less than in protected areas (Menon & Poirier, 1996). Again this is probably due to the abundance of food in protected areas, thus the group can spend more time resting, during which time juveniles are most likely to play, whereas in fragmented populations groups may have to spend more time foraging for food. Play behaviour varied between zoos, but this was more due to the social structure of groups, as some groups had more juveniles than others. Adults were also shown to exhibit greater rates of allogrooming and resting but less time in social interactions such as play compared to juveniles.

Enclosure complexity influences the activity of captive animals, particularly locomotion, foraging and play behaviour. For example, in captive ocelets (*Leopardus pardalis*), it was found that these cats were much less active than their wild counterparts, particularly as these cats are naturally nocturnal (Weller & Bennett, 2001). In captivity, they were fed their entire daily ration of food in the morning hours and thus the lack of a need to hunt for their own food at night decreased. However, the majority of cats did maintain the basic activity pattern of a free ranging cat and this meant that the ocelets were most active when visitors were not present. It was suggested that altering feeding practices and routines to encourage 'more "hunting" or food procurement behaviours' may increase the activity of the cats and change the times when they are most active. Lion-tailed macaques are not nocturnal, however, this study would have benefited from observations of groups starting at sunrise instead of starting observations at 09:00h (as was necessary for practical reasons). From studies in the wild on the Buton macaque, it was observed that groups were very active at sunrise and this activity decreased towards midday and then increased in the afternoon before settling in a sleeping tree (Irving-lewis, 2003). Indeed in wild lion-tailed macaques the time spent resting was significantly lower in the early morning (06:00h – 10:00h) (Menon & Poirier, 1996). Thus, the rate of activity recorded would possibly have been higher in the captive population if observations had been carried out at an earlier time.

In regards to enclosure complexity, enclosures that had extensive enrichment such as ropes, platforms, tyres, tunnels, feeding devices and so on, did encourage individuals to be more active particularly juveniles. Enclosure complexity can be modified to a species requirements', such as by adding extra height to the enclosure and changing the foraging substrate. When an orangutans' enclosure was modified to include four vertical levels, it encouraged the orangutans to use the upper canopy, and due to a flooded floor enabled this species to perform more natural behaviours, such as using vines to swing between canopy levels and thus act more like its wild arboreal counterparts (Herbert & Bard, 2000). Lion-tailed macaques are also arboreal species, however, in this study, one group (Zoo E) in particular spent the majority of its time on the ground. Their enclosure was an island with structures in place to add height to

the enclosure, however, the macaques only used this apparatus when they felt threatened such as when keepers were on the island to feed them. This enclosure did have an expanse of foraging material, water surrounding the island in which the macaques were observed catching fish in the summer and so on, so as there was no predation, this group may not have had the need to climb. If a group such as this was placed in a wild environment, there is a concern that they would not utilise their habitat extensively, in regards to arboreality. This needs to be considered when forming groups for reintroduction and highlights the point that as with all species planned for reintroduction, individuals need to be given an environment that is similar to their natural environment in order to gain appropriate skills to survive.

Thus, any form of enrichment, from increasing the variety of food types or changing the way that food is provided, to changes in the physical structures of enclosures is a key to promoting 'natural' behaviour in captive animals (Newberry, 1995).

Welfare of captive lion-tailed macaques

Another problem in the European captive lion-tailed macaque population is that a high number of males have had to be taken out of a group until another group requires a dominant male. However, this means that many potential breeding males are being housed in pairs or singly. In a previous study, an attempt was made to house five adult male lion-tailed macaques together, in a group with a number of females, where each individual had been housed singly for the previous four years and had not been housed with adult males since adolescence (Clarke *et al*, 1995). When these males were group housed it was found that they showed no affiliative social behaviour towards each other (e.g. proximity, contact, grooming, non aggressive approach). They kept the maximum distance from each other by actively avoiding and constantly monitoring each others movements and locomotion. This group was disbanded at the end of the study, as group living was not suitable for these males, especially the lowest ranked individual, who was rarely observed feeding with the rest of the group. Thus, Clarke *et al* (1995) concluded that these males, due to previous experience, appeared to be highly intolerant of one another

and also relatively asocial even in their relationships with females. This study highlights possible problems with planned reintroduction programmes for 'all male' groups. At present, a pilot study is underway in Portugal, where attempts are being made to house an 'all male' captive group of lion-tailed macaques, in which three of the males have been housed together before for a number of years and so far this project seems to be successful (Kaumanns pers. com).

It is often assumed that animals suffer if they cannot perform behaviours seen in wild conspecifics (Veasey *et al*, 1996). Barnard & Hurst (1996) state that 'the welfare of an animal can be interpreted only in terms of what natural selection has designed an organism to do and how circumstances impinge on its functional design'. If an animal is placed in a barren exhibit with little enrichment it is predicted that the welfare of that animal is very poor and is more likely that an animal will perform more abnormal stereotypical behaviours (McPhee *et al*, 1998). However, if an animal is placed in a large enclosure full of enrichment, the welfare of that animal is considered to be improved. Indeed, enrichment techniques enable animals to be exposed to a variety of stimului, thus promoting the welfare of that species. In lion-tailed macaques, it is clear that when in captivity, this species, clearly benefits from a larger, more complex enclosure. However, what many visitors do not realise when they go to institutions to admire captive animals, despite gaining an education on different species from around the world they can have a negative impact on the welfare of captive species.

Visitor effects

As mentioned briefly, the presence of visitors tends to interrupt mating between individual lion-tailed macaques, thus possibly affecting the reproductive success of this species in captivity. Lion-tailed macaques are naturally shy primates and thus could benefit from some form of visitor barrier that enables visitors to see into the enclosure but enables the macaques to remain private. For example, when a camouflage net was placed in the viewing area of a gorilla exhibit it was found that the gorillas exhibited significantly lower levels of conspecific-directed aggression and stereotypic behaviours (Blaney & Wells, 2004). From a visitors' perception the

gorillas were said to look more exciting and less aggressive. Thus, this introduction of netting had a positive effect on the gorillas behaviour, as it resulted in the reduction in behaviours that are typically induced by large groups of visitors, such as aggression and it also improved the public perceptions of the animals and their environment. Thus, it is possible that the reproductive success could be increased by giving lion-tailed macaques more privacy and as previously stated altering the nutrition to ensure that females are getting the correct requirements during pregnancy and when lactating.

Another finding from this study was that visitors caused an alteration in the diet of lion-tailed macaques through feeding them inappropriate items such as; crisps, lollipops, even cans of fruit. These could have detrimental effects on the lion-tailed macaques health if consumed. Despite plenty of signs in all zoos asking visitors to refrain from feeding the animals, it still occurred frequently. The feeding of the lion-tailed macaques by visitors also increased aggression within groups as individuals would fight over any inappropriate item they had received. Thus enclosure design needs to be re-assessed at institutions where this problem is prominent by placing barriers so that no physical contact can occur between visitors and the animals, however this is not always practical. Aggression was also observed in the form of alarm vocalizations. These were produced, usually by a dominant individual and were produced in situations such as when the vet or certain keepers were in close proximity to the enclosure. In general, the highest frequency of these calls were exhibited by groups that had individuals who had received extensive veterinary treatment.

Comparing the behaviour of zoo-housed animals with their wild conspecifics is not necessarily an accurate method for assessing welfare. Many behaviours are stimulus driven rather than internally generated, thus the non-performance of some wild-type behaviours does not necessarily compromise that individuals welfare (Veasey *et al*, 1996). The study population were found to exhibit behaviours that were the same as their wild counterparts and no stereotypical behaviours were recorded. The only unusual behaviour reported in this study was that of the 'hand to eye' behaviour

which was exhibited by only three older females. It is believed that this was not a stereotypic behaviour as it was performed only when individuals were waiting for food and thus looking for the keeper, or when they were searching for food from above. It possibly indicates an eyesight problem in these macaques although this is only hypothetical and thus needs further investigation.

Reintroduction programmes

Reintroduction programmes are widespread but have had low success rates, particularly when captive animals have been used (Mathews *et al*, In press). Reintroduction programmes however could be the best method of saving lion-tailed macaques from becoming extinct. In order for these programmes to be more successful, several factors need to be considered.

It has been seen in this study that captive lion-tailed macaques appear to be quite aggressive to neighbouring species. In the wild, lion-tailed macaques have been reported to share their habitat with a threatened species the nilgiri langur (*Presbytis johnii*) where both feed on the same resources and in fact nilgiri langurs depend on lion-tailed macaques to gain access to *Cullenia* fruits as previously mentioned in Chapter 1, 1.1.3. Thus, the issue arises of whether a reintroduced group, which have never seen nilgiri langurs or have never lived in close proximity to another species would successfully co-exist or whether detrimental effects would be caused in either species such as physical aggression between groups resulting in individual mortality.

To assess the suitability of captive bred animals for release, Mathews *et al* (In press) compared the behaviours of wild-bred and captive-bred bank voles (*Clethrionomys glareolus*) in identical novel environments. It was found that captive-bred voles did display some wild-type behaviours such as nest building and burrowing, but they were unable to utilize a key food resource and were less dominant than wild-bred. It was suggested that this method of comparison could be applied to any species of conservation concern, in order to rank available animals in terms of likely suitability of release. In relation to lion-tailed macaques, this could be a useful method of establishing which individuals would be best for reintroduction. However, taking

individuals with the most favourable and most diverse genes were taken from the captive population to form a possible reintroduction group, this would not be the best option, as it has already been seen that individuals that do not know each other tend to avoid each other, rather than try and establish relationships. This would also mean that the 'quality' of the captive stock would decrease and if the reintroduced group was wiped out from various factors such as disease, these genes would be lost. They would not necessarily by chance have the correct genes and thus ability to adapt and survive through such stochastic events.

There is also the question of whether reintroduced male lion-tailed macaques would actually disperse once reaching maturity and also if they would have the necessary skills to successfully join another wild group. Thus when considering reintroduction programmes for lion-tailed macaques, the suitability of individuals should be assessed at a group level and not necessarily be composed of individuals with the best genes from the population as a whole. As seen in the current study, there is variation in the captive environment of lion-tailed macaques between institutions and this appears to influence the lion-tailed macaques' behaviour. Increased variation in the lion-tailed macaques' captive environment along, with pre-release training such as learning appropriate foraging skills, could be the answer to increase the success of reintroducing this species (McPhee, 2003).

Although the current study has raised several concerns over possible complications regarding the reintroduction of the lion-tailed macaque, the reintroduction of primates can be successful. For example, the black howler monkeys (*Alouatta pigra*) was reintroduced into the Cockscomb Basin Wildlife Sanctuary, Belize. The appropriate management plans before release were followed, that is the habitat was surveyed and an estimate was made on how many howler monkeys this habitat could support and it was ensured that all monkeys due to be released were in good health and fitted with radio telemetry so that they could be tracked once released and so on. Sixty-two howler monkeys were released however, 93% survived for 30 days, 84% survived for at least 6 months and 80% survived for one year. The translocated howler monkeys showed high survivability, low dispersal (0-9km, mostly <3km) and

high infant survivability (70%). It is now believed that with some demographic and stochastic luck, the black howler monkeys now living in the Cockscomb Basin have a reasonable chance to re-establish a viable population (Koontz, 1997).

Therefore, if captive-bred lion-tailed macaques attain the appropriate life skills through pre-training, the group is made up of related individuals and has been an established group for a number of years with a high rate of reproductive success, and if the group have been familiarised with the proposed reintroducion habitat, (i.e. by enclosing the captive group in part of this habitat for a certain duration before release), then perhaps this species could successfully re-establish itself in the wild. Using captive groups as a model and comparing them to their wild counterparts could identify the possible constraints that a captive population would face before being released and thus appropriate changes could be made to ensure that the reintroduced group had the best chance of survival.

Conclusion

From this study it can be concluded that

- The social structure, spatial relationships and activity budgets varied between captive groups of lion-tailed macaques.
- Social structure varied between zoos due to the difference in group size.
- Although not significant, females that were related to the dominant female of the group appeared to spend time in closer proximity to her than unrelated females.
- Wild populations, if fragmented, may have similar restrictions to those of captive groups. Consequently, the reproductive rate may decrease and dominance hierarchy may be disrupted in fragmented populations.
- Differences were found between the activity budgets of wild and captive populations, mainly in the time spent resting.
- Activity budgets varied between zoos with some more closely mimicking that of wild groups than others.

- The added benefits of having grass as a foraging substrate by providing the macaques with natural resources such as birds and rodents could influence the nutrition of individuals and in turn could have an effect on the reproductive success of lion-tailed macaques in captivity.
- Enclosure size and complexity mainly influenced the time spent in active behaviours.
- All zoos in this study had barriers in place between visitors and animals, however many of these were found to be ineffective, with the result that visitors often fed inappropriate items to the lion-tailed macaques.

Recommendations

Various recommendations can be made from this study regarding the possible reintroduction of lion-tailed macaques.

Captive lion-tailed macaques

- As social structure is affected by group size and spatial relationships between individuals are influenced by size of enclosure, sufficient space must be provided to house large groups and to enable individuals to distance themselves from each other if necessary.
- The most appropriate type of foraging material provided needs to be assessed, as so far it seems that grass is most favourable and this encourages foraging activity.
- As it is thought that the nutrition of pregnant females affects their reproductive success, females need to be closely monitored during pregnancy. Weight gain could be monitored during pregnancy by training the females to move onto a weighing platform for a food reward and supplementary feeding could be given if required.
- Groups in bigger and more complex enclosures showed more activity than those in smaller, less complex enclosures. Enclosures design should incorporate enrichment that stimulates a wide range of natural behaviours.

- The impact of visitors in regards to the diet of lion-tailed macaques would need to be altered in some institutions, perhaps by constructing a physical barrier between the animals and the public.

Reintroduction of lion-tailed macaques

- The size and complexity of enclosures could simulate the environment that wild fragmented populations are facing, in terms of the restrictions of habitat use and food resources. Thus the study of captive populations could be a useful indicator regarding the outcome of populations inhabiting these fragmented habitats. Wild fragmented populations have the added problem of a restriction on male dispersal, thus if interconnecting forests were constructed between fragments this would enable males to immigrate and emigrate between groups and thus the genetic diversity of these populations would be able to be maintained.
- The individuals with the most favourable and diverse genes are not necessarily the most suitable for reintroduction. Individuals and groups should therefore be assessed on their suitability for reintroduction based on genetics and previous reproductive success.

Future work

- The nutrition of captive lion-tailed macaques should be assessed to see if there is any correlation between the nutritional status of an individual and its reproductive success.
- In order for captive groups of lion-tailed macaques to be used as a viable model to predict changes in wild fragmented populations, a larger number of captive groups need to be studied, not only in the European population, but also from institution in other parts of the world, for example, America.
- In order to make a suitable comparison, studies of wild populations particularly those populations occupying fragmented habitats must be carried out.

- Ways of increasing the reproductive success of the captive population need to be addressed particularly if this population will act as the stock for future reintroduction programmes, which, providing the issues mentioned previously can be managed, seems the most viable solution to conserving this endangered species.

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Appendix 1

Social structure, activity budgets and spatial relationships of the British and Irish captive population of lion-tailed macaques (*Macaca silenus*)

Zoo Survey

1) How many Lion-tailed macaques (*M. silenus*) are there in the zoo collection?

2) What is the group composition of these macaques (i.e. the ratio of males to females, number of infants etc)?

3) What is the rearing history of the adult macaques within the group?

4) How many of the macaques are involved in a captive breeding programme?

5) What is the diet of these macaques?

6) Is there seasonal variation within this diet?

7) What are the feeding times?

8) On average how much does it cost to feed these macaques per day?

9) Do the macaques receive additional vitamin supplements etc besides that contained in their food?

10) How long do the macaques spend on exhibit?

11) Do the macaques receive any additional immunisation, parasitic treatments etc?

12) What type of enrichment does the enclosure have (i.e. climbing apparatus, feeding baskets etc)?

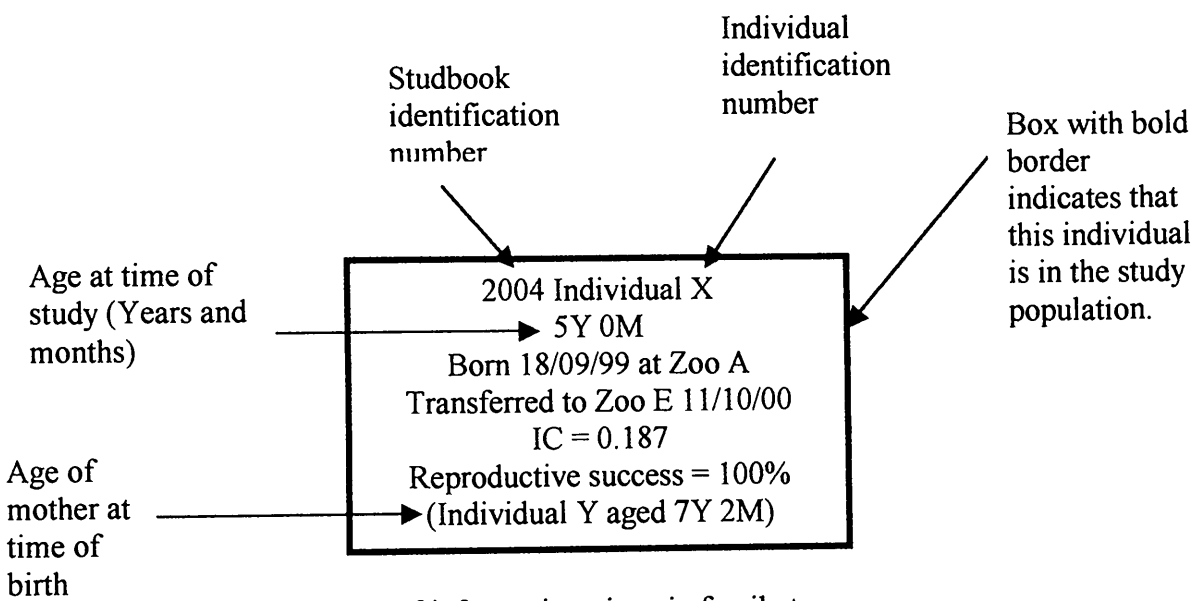
Appendix 2

Family trees for Zoos A – E

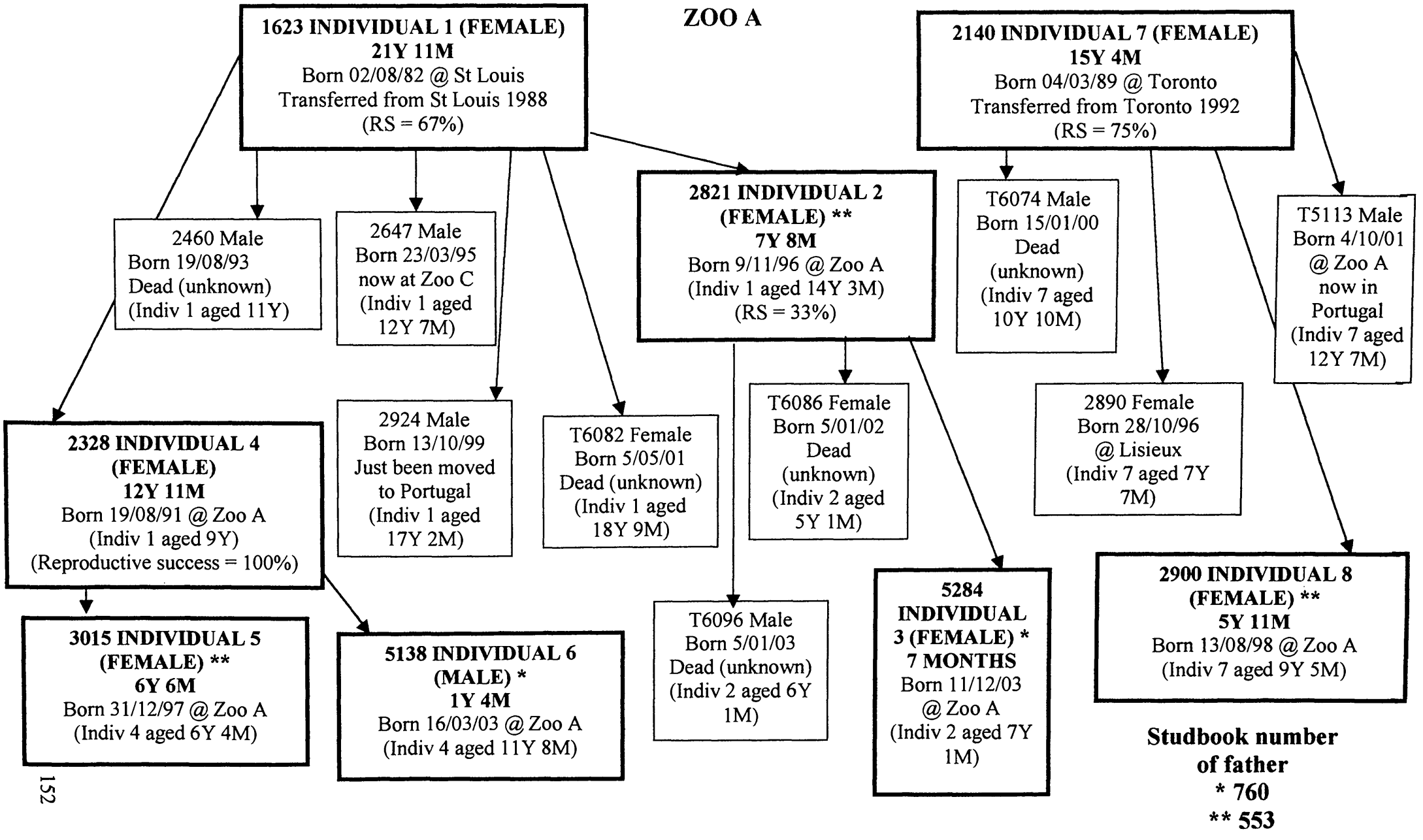
Family trees show relationships between individuals within each zoo (bold) and also includes individuals that have died or been moved to another institution.

For each individual the following information is given:

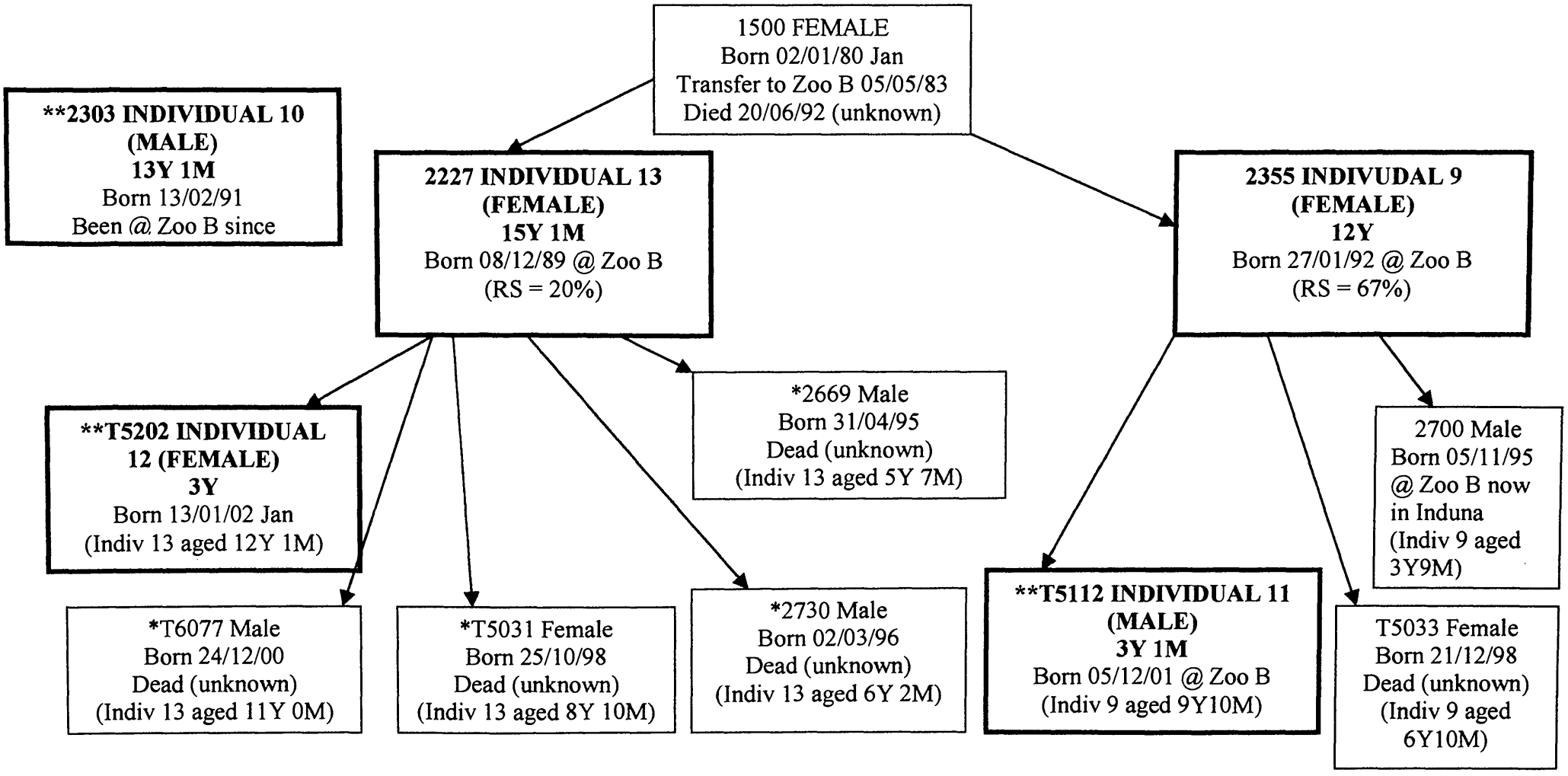
- Studbook identification number and individual identification number within study population (see Chapter 2, Table 2.1)
- Age at time of study (Years and months)
- Date of birth
- Place of birth
- If applicable name of institution moved to or cause of death
- Inbreeding coefficient (IC) (see Chapter 2, 2.2). Unless otherwise stated, IC = 0.
- Reproductive success of females where applicable (see Chapter 3, 3.2.1)
- Age of mother at time of birth



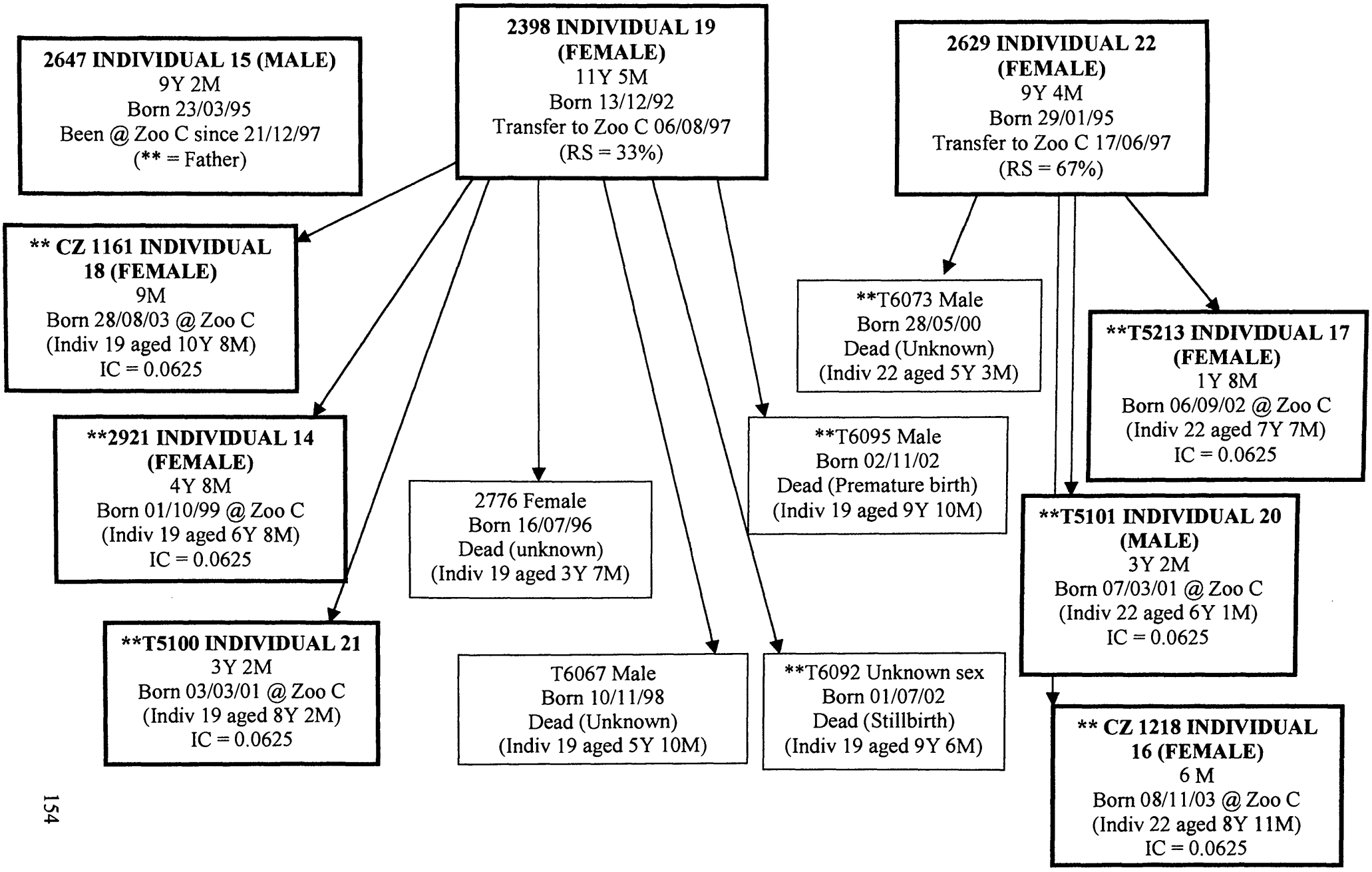
Example of information given in family trees


ZOO A
1623 INDIVIDUAL 1 (FEMALE)
21Y 11M
Born 02/08/82 @ St Louis
Transferred from St Louis 1988
(RS = 67%)
2140 INDIVIDUAL 7 (FEMALE)
15Y 4M
Born 04/03/89 @ Toronto
Transferred from Toronto 1992
(RS = 75%)
2460 Male
Born 19/08/93
Dead (unknown)
(Indiv 1 aged 11Y)
2647 Male
Born 23/03/95
now at Zoo C
(Indiv 1 aged
12Y 7M)
2821 INDIVIDUAL 2
(FEMALE) **
7Y 8M
Born 9/11/96 @ Zoo A
(Indiv 1 aged 14Y 3M)
(RS = 33%)
T6074 Male
Born 15/01/00
Dead
(unknown)
(Indiv 7 aged
10Y 10M)
T5113 Male
Born 4/10/01
@ Zoo A
now in
Portugal
(Indiv 7 aged
12Y 7M)
2328 INDIVIDUAL 4
(FEMALE)
12Y 11M
Born 19/08/91 @ Zoo A
(Indiv 1 aged 9Y)
(Reproductive success = 100%)
2924 Male
Born 13/10/99
Just been moved
to Portugal
(Indiv 1 aged
17Y 2M)
T6082 Female
Born 5/05/01
Dead (unknown)
(Indiv 1 aged
18Y 9M)
T6086 Female
Born 5/01/02
Dead
(unknown)
(Indiv 2 aged
5Y 1M)
2890 Female
Born 28/10/96
@ Lisieux
(Indiv 7 aged 7Y
7M)
3015 INDIVIDUAL 5
(FEMALE) **
6Y 6M
Born 31/12/97 @ Zoo A
(Indiv 4 aged 6Y 4M)
5138 INDIVIDUAL 6
(MALE) *
1Y 4M
Born 16/03/03 @ Zoo A
(Indiv 4 aged 11Y 8M)
T6096 Male
Born 5/01/03
Dead (unknown)
(Indiv 2 aged 6Y
1M)
5284
INDIVIDUAL
3 (FEMALE) *
7 MONTHS
Born 11/12/03
@ Zoo A
(Indiv 2 aged 7Y
1M)
2900 INDIVIDUAL 8
(FEMALE) **
5Y 11M
Born 13/08/98 @ Zoo A
(Indiv 7 aged 9Y 5M)
Studbook number
of father
* 760
** 553

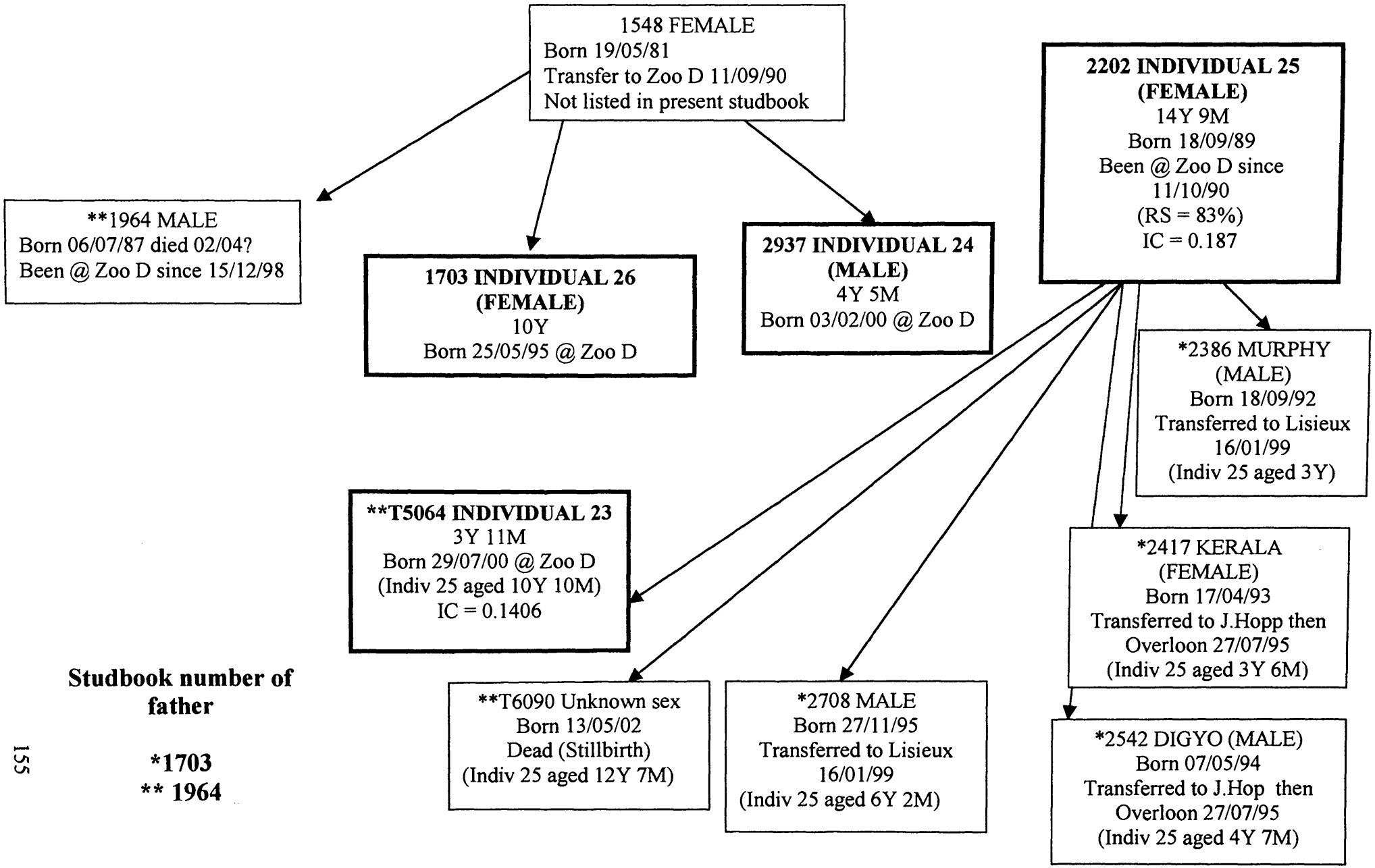
ZOO B


1500 FEMALE
Born 02/01/80 Jan
Transfer to Zoo B 05/05/83
Died 20/06/92 (unknown)
**2303 INDIVIDUAL 10
(MALE)
13Y 1M
Born 13/02/91
Been @ Zoo B since
2227 INDIVIDUAL 13
(FEMALE)
15Y 1M
Born 08/12/89 @ Zoo B
(RS = 20%)
2355 INDIVUDAL 9
(FEMALE)
12Y
Born 27/01/92 @ Zoo B
(RS = 67%)
**T5202 INDIVIDUAL
12 (FEMALE)
3Y
Born 13/01/02 Jan
(Indiv 13 aged 12Y 1M)
*2669 Male
Born 31/04/95
Dead (unknown)
(Indiv 13 aged 5Y 7M)
2700 Male
Born 05/11/95
@ Zoo B now
in Induna
(Indiv 9 aged
3Y9M)
*T6077 Male
Born 24/12/00
Dead (unknown)
(Indiv 13 aged 11Y 0M)
*T5031 Female
Born 25/10/98
Dead (unknown)
(Indiv 13 aged 8Y 10M)
*2730 Male
Born 02/03/96
Dead (unknown)
(Indiv 13 aged 6Y 2M)
**T5112 INDIVIDUAL 11
(MALE)
3Y 1M
Born 05/12/01 @ Zoo B
(Indiv 9 aged 9Y10M)
T5033 Female
Born 21/12/98
Dead (unknown)
(Indiv 9 aged
6Y10M)

ZOO C


2647 INDIVIDUAL 15 (MALE)
9Y 2M
Born 23/03/95
Been @ Zoo C since 21/12/97
(** = Father)
2398 INDIVIDUAL 19 (FEMALE)
11Y 5M
Born 13/12/92
Transfer to Zoo C 06/08/97
(RS = 33%)
2629 INDIVIDUAL 22 (FEMALE)
9Y 4M
Born 29/01/95
Transfer to Zoo C 17/06/97
(RS = 67%)
** CZ 1161 INDIVIDUAL 18 (FEMALE)
9M
Born 28/08/03 @ Zoo C
(Indiv 19 aged 10Y 8M)
IC = 0.0625
**T6073 Male
Born 28/05/00
Dead (Unknown)
(Indiv 22 aged 5Y 3M)
**T5213 INDIVIDUAL 17 (FEMALE)
1Y 8M
Born 06/09/02 @ Zoo C
(Indiv 22 aged 7Y 7M)
IC = 0.0625
**2921 INDIVIDUAL 14 (FEMALE)
4Y 8M
Born 01/10/99 @ Zoo C
(Indiv 19 aged 6Y 8M)
IC = 0.0625
2776 Female
Born 16/07/96
Dead (unknown)
(Indiv 19 aged 3Y 7M)
**T6095 Male
Born 02/11/02
Dead (Premature birth)
(Indiv 19 aged 9Y 10M)
**T5101 INDIVIDUAL 20 (MALE)
3Y 2M
Born 07/03/01 @ Zoo C
(Indiv 22 aged 6Y 1M)
IC = 0.0625
**T5100 INDIVIDUAL 21
3Y 2M
Born 03/03/01 @ Zoo C
(Indiv 19 aged 8Y 2M)
IC = 0.0625
T6067 Male
Born 10/11/98
Dead (Unknown)
(Indiv 19 aged 5Y 10M)
**T6092 Unknown sex
Born 01/07/02
Dead (Stillbirth)
(Indiv 19 aged 9Y 6M)
** CZ 1218 INDIVIDUAL 16 (FEMALE)
6 M
Born 08/11/03 @ Zoo C
(Indiv 22 aged 8Y 11M)
IC = 0.0625

ZOO D



Studbook number of father

***1703**
**** 1964**

ZOO E

1544 INDIVIDUAL 33
(MALE)
22Y 10M
Born 21/04/81
Been @ Fota since 12/09/00

1711 INDIVIDUAL 34
(FEMALE)
20Y
Born 24/02/84
Transfer to Zoo E 16/01/87
(RS = 100%)

1702 FEMALE
Born 10/11/83
Transfer to Zoo E 16/08/85
Not listed in present studbook

2660 MALE
Born 01/07/95
Transfer to Zoo D
12/09/00. Been
transferred again.

2007 Male
Born 19/01/88
Dead (Unknown)
(Indiv 34 aged 3Y 10M)

2922 INDIVIDUAL 35
(FEMALE)
4Y 4M
Born 0710/99 @ Zoo D
(Indiv 34 aged 15Y 7M)
(RS = 100%)

2361 INDIVIDUAL 31
(FEMALE)
12Y
Born 29/02/92 @ Fota
(RS = 60%)

***2874 INDIVIDUAL 29**
(FEMALE)
6Y 2M
Born 20/12/97 @ Zoo D
(RS = 100%)

*2526 Male
Born 22/03/94
Dead (Unknown)
(Indiv 34 aged 10Y 0M)

*2883
Male
Born
13/02/98
Transfer to
Munster

****3513 Male**
2M
Born 04/12/03
(Indiv 34 aged
4Y 2M)

****3509 FEMALE**
3M
Born 17 Nov 2003
(Indiv 31 aged 12 Y)

****T5220 INDIVIDUAL**
30 (FEMALE)
1Y 2M
Born 3 Dec 2002 @ Fota
(Aged 4Y 11M)

*2691 Male
Born 19/10/95
Dead (Unknown)
(Indiv 34 aged 11Y 7M)

****T5205 INDIVIDUAL**
36 (FEMALE)
1Y 11M
Born 02/03/02 @ Zoo D
(Indiv 34 aged 18Y 0M)

****T5206 INDIVIDUAL 37**
(MALE) 1Y 11M
Born 26/03/02 @ Zoo D
(Indiv 31 aged 10Y 0M)

T6031 Female
Born 8/11/95
Dead (Unknown)
(Indiv 31 aged 3Y 8M)

*2856 Male
Born 19 Dec 1996
Transfer to Ramatgan 05/09/00
(Indiv 34 aged 12Y 9M)

2366 INDIVIDUAL 27
(FEMALE)
11Y 10M
Born 23/04/92 @ Zoo D
(Indiv 34 aged 8Y 2M)
(RS = 100%)

***2954 INDIVIDUAL 32**
(FEMALE)
3Y 3M
Born 15/11/00 @ Zoo D
(Indiv 31 aged 8Y*M19D)

T6045 Male
Born 22/12/96
Dead (Unknown)
(Indiv 31 aged 4Y 9M)

****T5219 INDIVIDUAL 28**
(FEMALE)
1Y 3M
Born 14/11/02 @ Zoo E

*2906 Male
Born 07/11/98
Transfer to Munster
(Indiv 31 aged 6Y 8M)

156

Studbook number of father
*** 1754**
**** 1544**

Appendix 3

Figure 1. Map of indoor and outdoor lion-tailed macaque enclosure for Zoo A (not to scale).

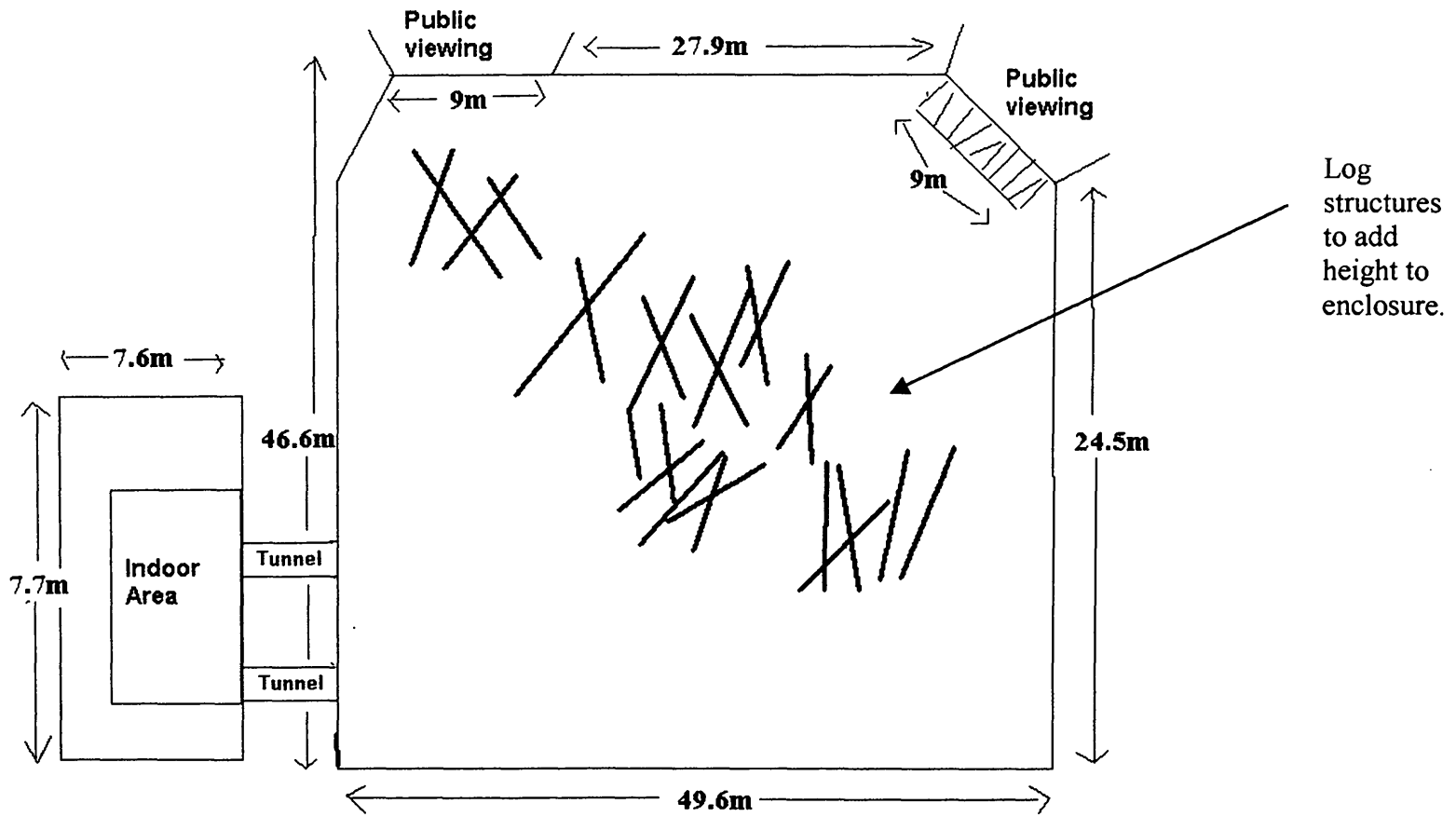


Figure 2a. Map of indoor lion-tailed macaque enclosure for Zoo B.

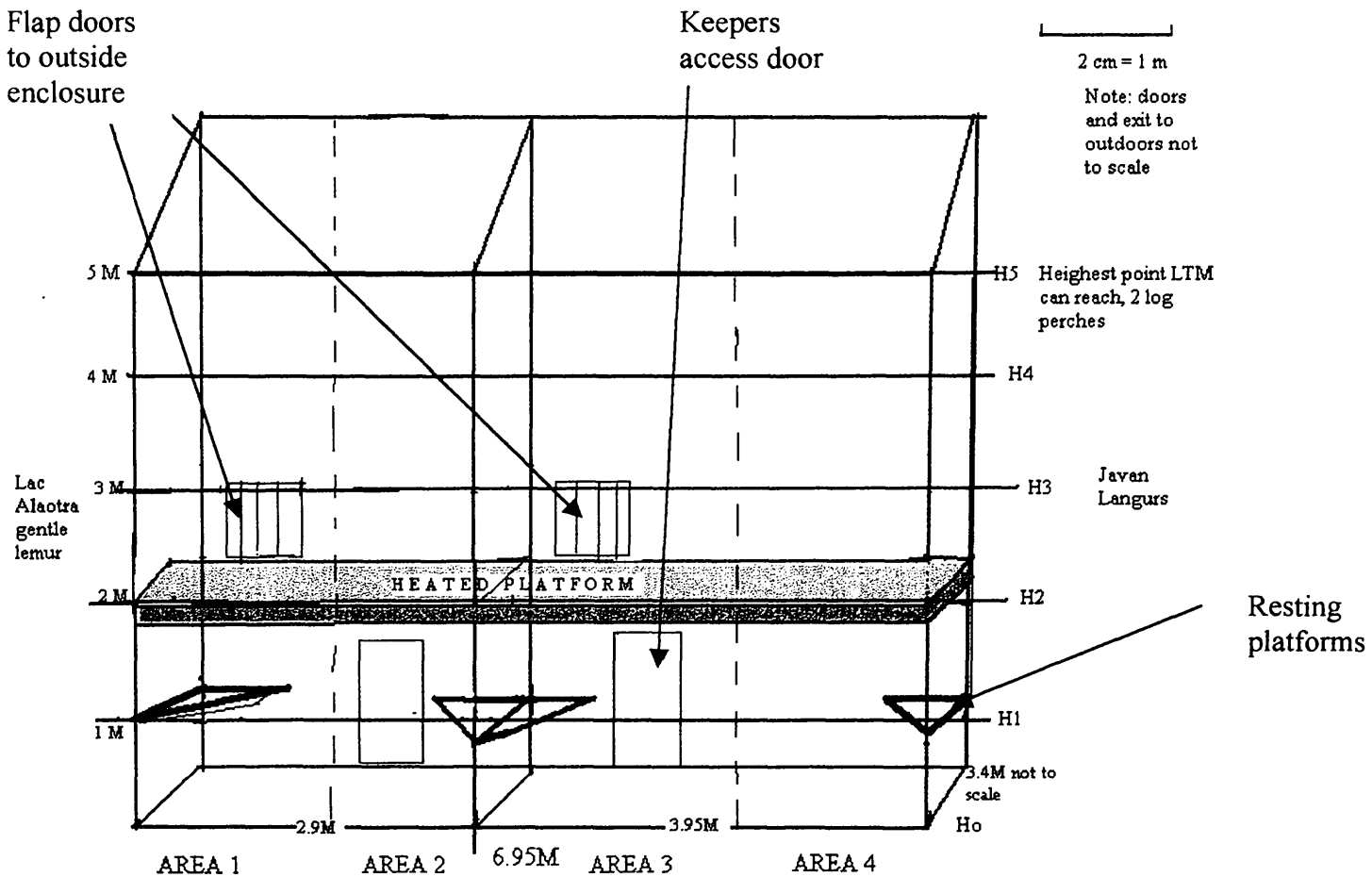


Figure 2b. Map of outdoor lion-tailed macaque enclosure for Zoo B.

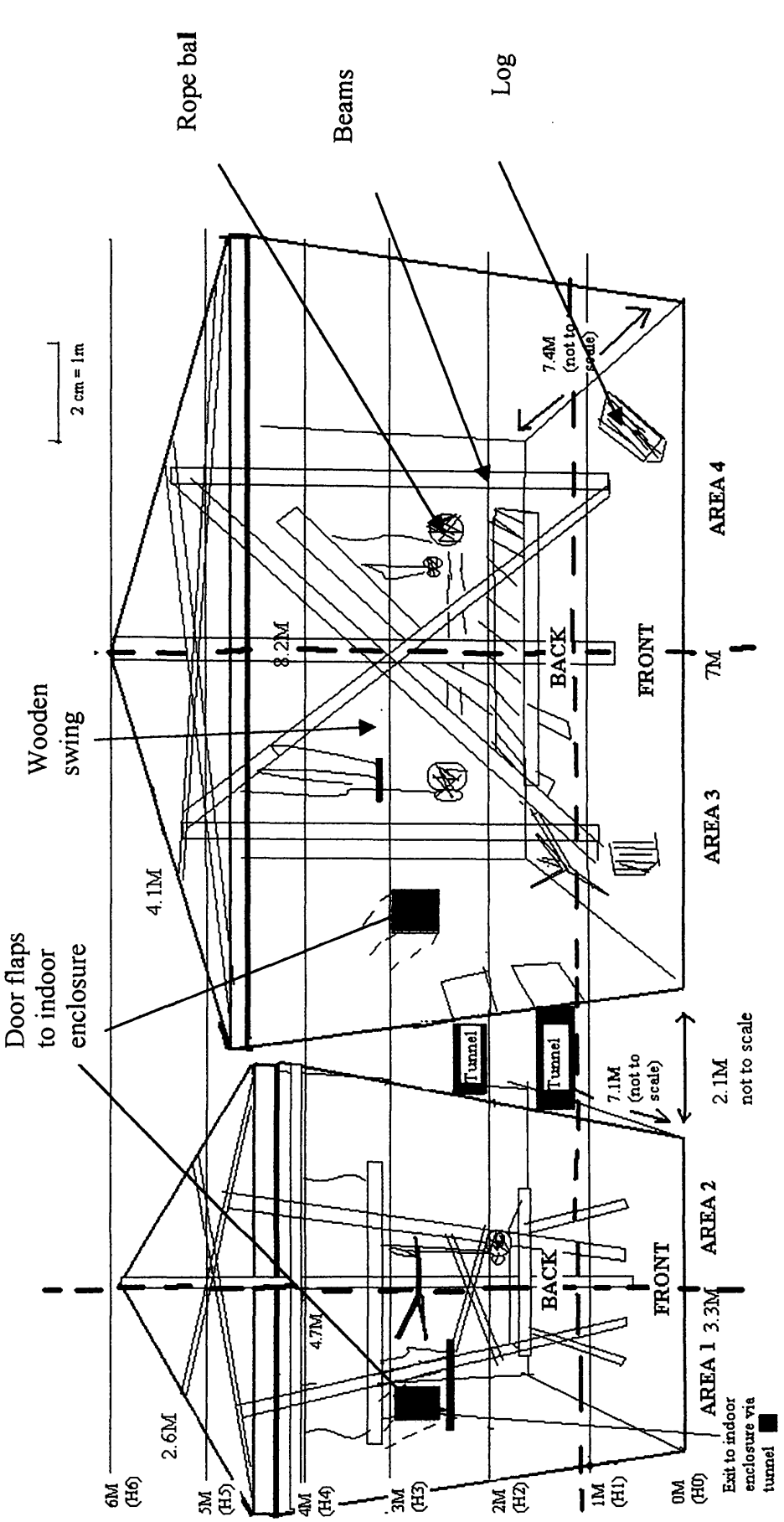


Figure 3a. Map of indoor lion-tailed macaque enclosure for Zoo C (not to scale).

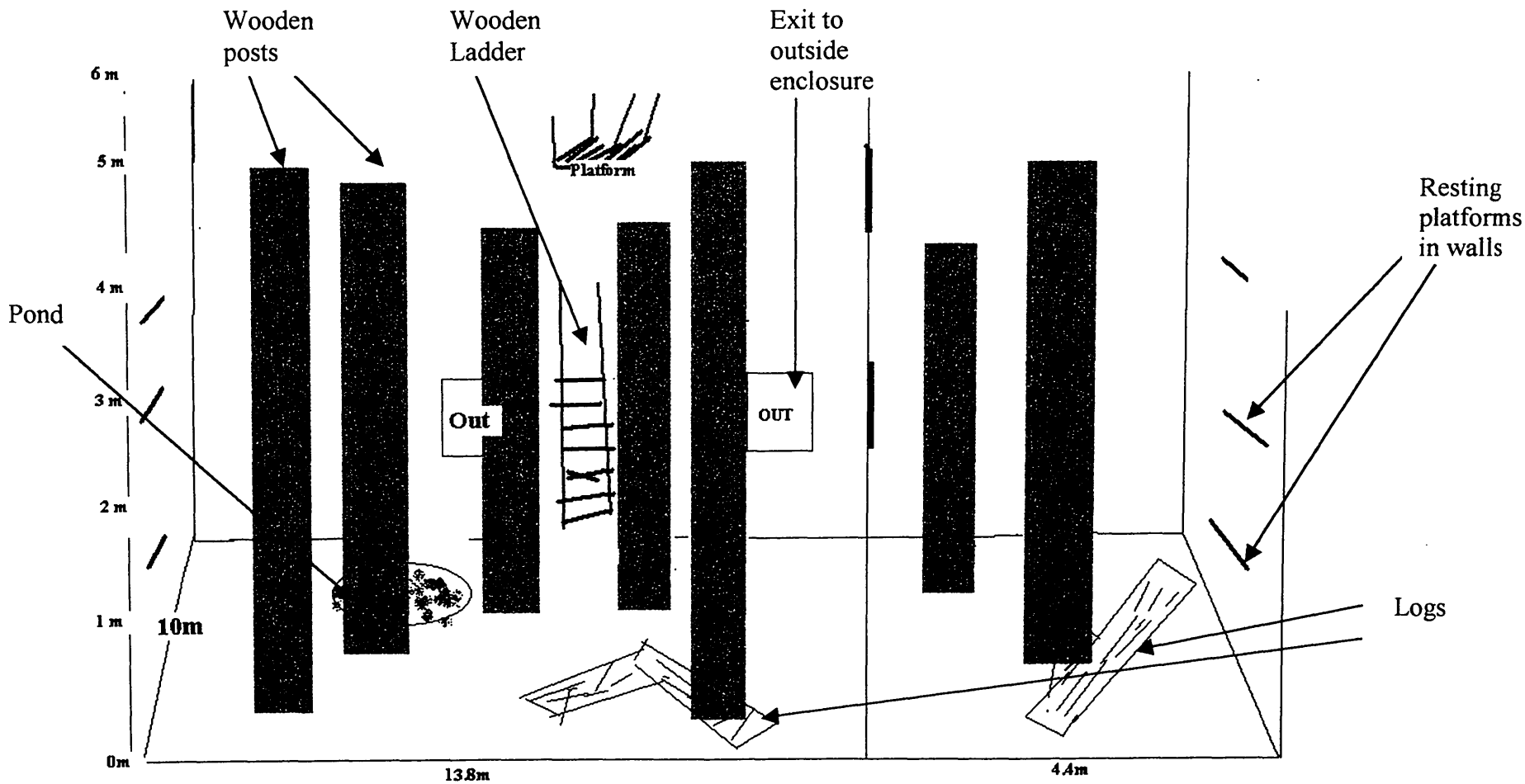


Figure 3b. Map of outdoor lion-tailed macaque enclosure for Zoo C (not to scale).

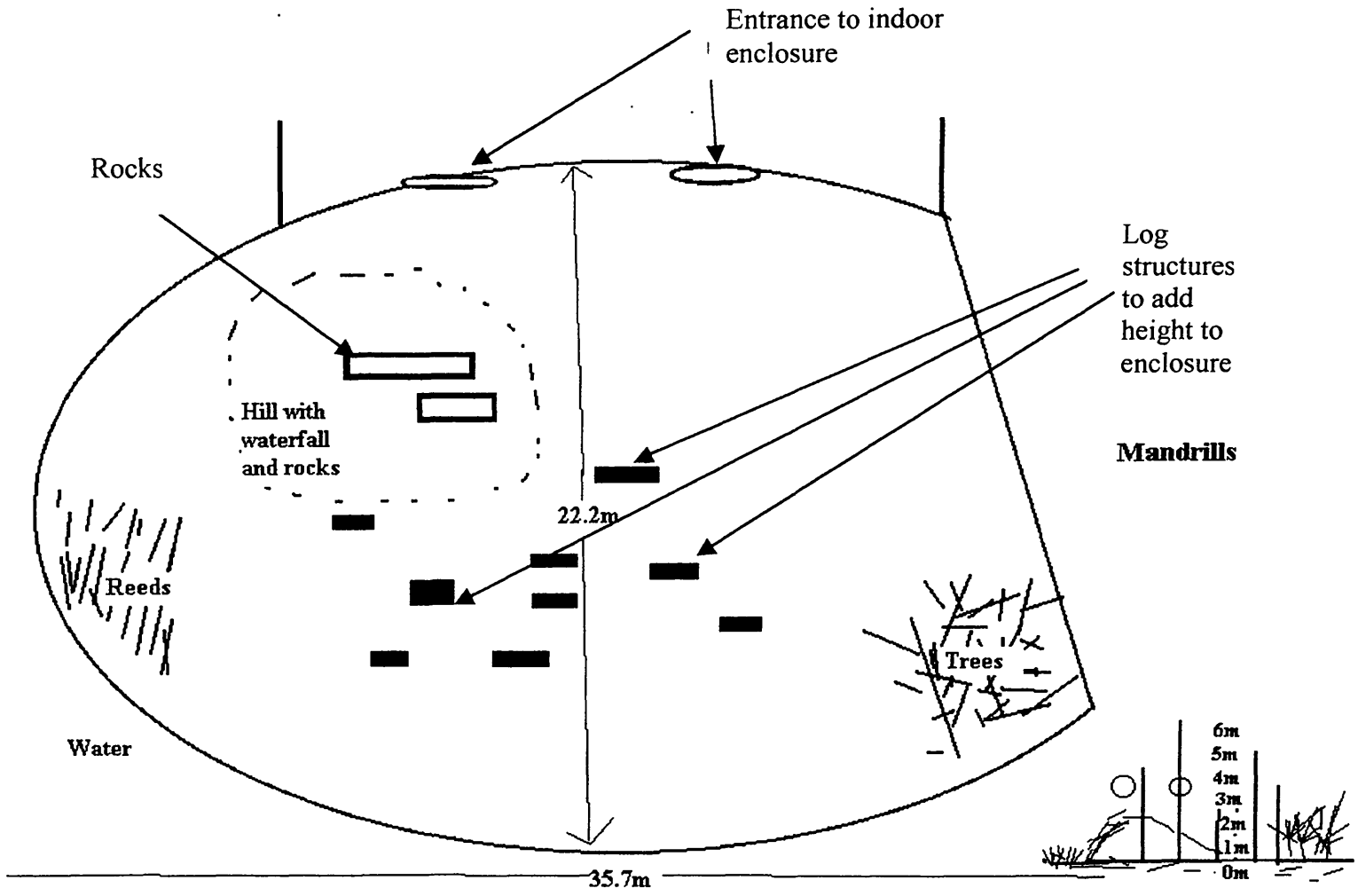


Figure 4. Map of lion-tailed macaque enclosure for Zoo D (not to scale).

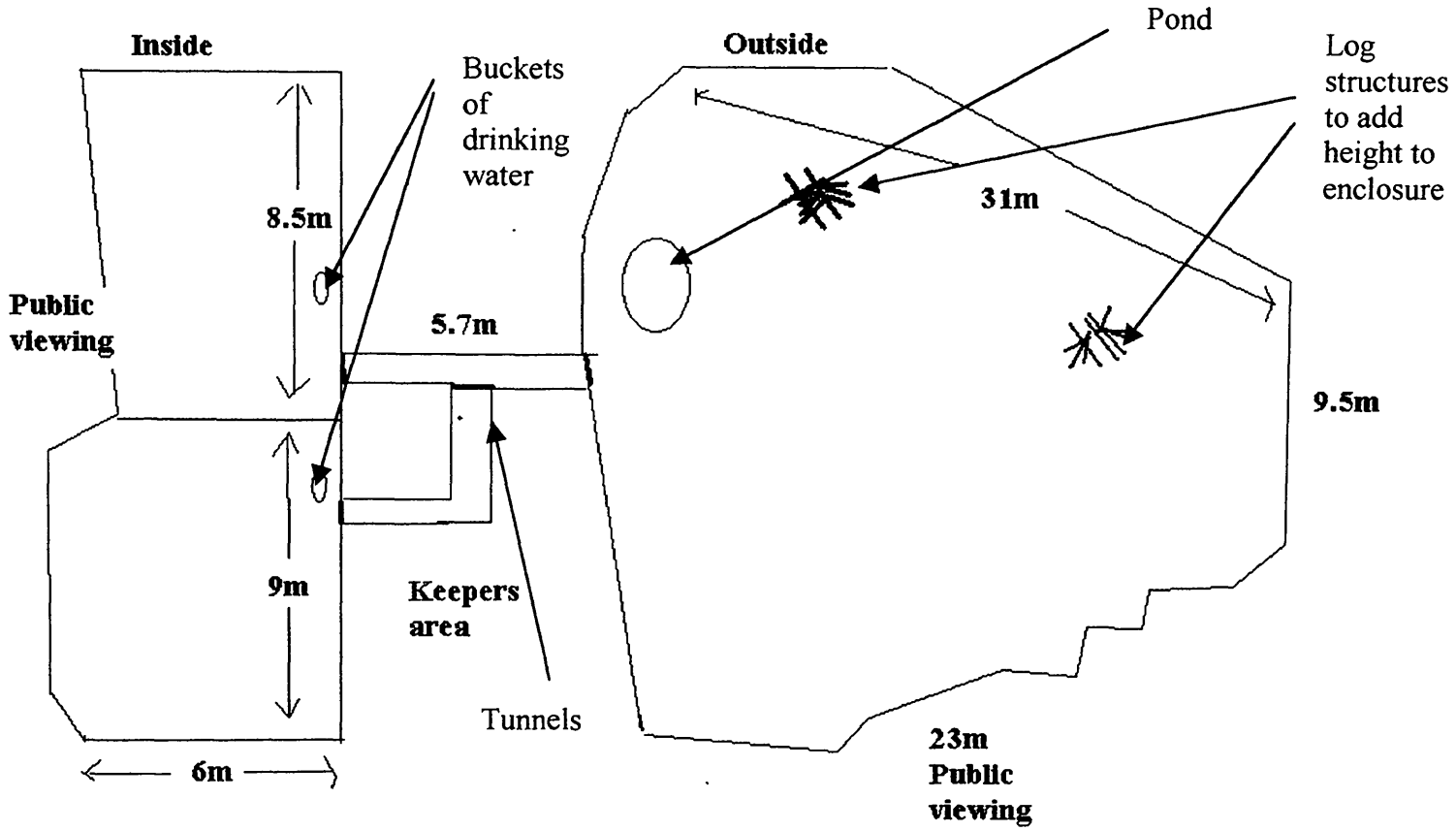
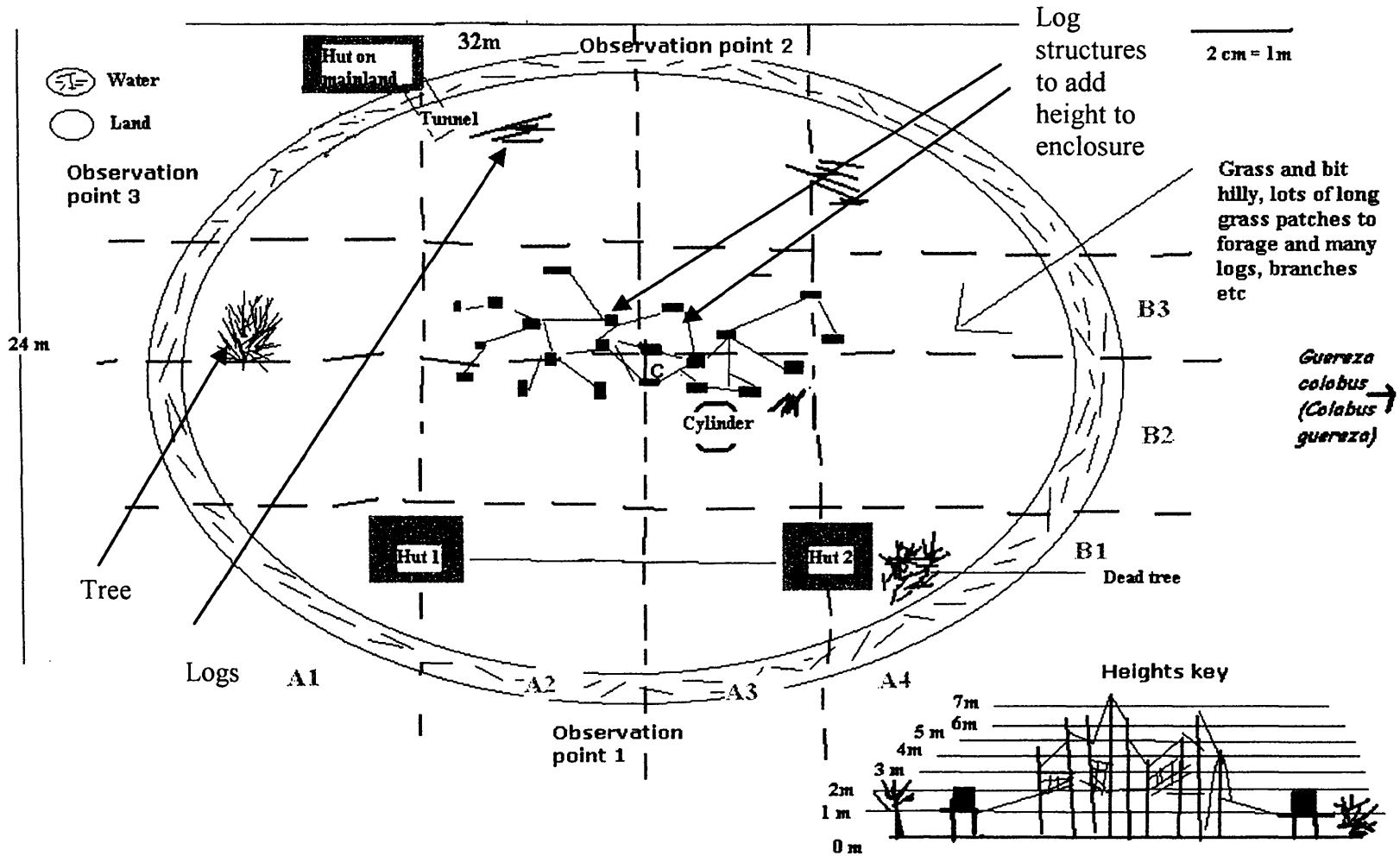


Figure 5. Map of lion-tailed macaque enclosure for Zoo E.



Appendix 4
(Chapter 3 – Social Structure and Spatial relationships)

Table I. Average separation distances between individuals at Zoo A (including standard errors)

ZOO A								
Average distances								
(Meters)								
INDIVIDUALS	1	4	5	2	3	6	7	8
1	0	14.33 ± 1.37	15.78 ± 1.10	11.69 ± 1.48	12.79 ± 1.23	14.33 ± 1.33	16.03 ± 1.50	18.05 ± 1.57
4	14.33 ± 1.37	0	9.85 ± 0.68	9.63 ± 0.82	9.35 ± 0.84	8.85 ± 1.23	17.73 ± 1.62	13.89 ± 1.06
5	15.78 ± 1.10	9.85 ± 0.68	0	10.81 ± 0.67	10.63 ± 0.54	11.12 ± 0.69	18.85 ± 1.63	14.37 ± 1.06
2	11.69 ± 1.48	9.63 ± 0.82	10.81 ± 0.67	0	3.85 ± 0.299	9.19 ± 0.66	15.78 ± 1.62	14.14 ± 1.08
3	12.79 ± 1.23	9.35 ± 0.84	10.64 ± 0.54	3.85 ± 0.299	0	8.24 ± 0.68	15.78 ± 1.58	13.73 ± 1.06
6	14.33 ± 1.33	8.85 ± 1.23	11.12 ± 0.69	9.19 ± 0.66	8.24 ± 0.68	0	15.31 ± 1.42	13.45 ± 1.11
7	16.03 ± 1.50	17.73 ± 1.62	18.85 ± 1.63	15.78 ± 1.62	15.78 ± 1.58	15.31 ± 1.42	0	17.74 ± 1.84
8	18.05 ± 1.57	13.89 ± 1.06	14.37 ± 1.06	14.14 ± 1.08	13.73 ± 1.06	13.45 ± 1.11	17.74 ± 1.84	0

Table II. Average separation distances between individuals at Zoo B (including standard errors).

ZOO B					
Average distances					
(Meters)					
INDIVIDUALS	10	13	9	12	11
10	0	2.37 ± 0.14	2.71 ± 0.21	2.71 ± 0.51	2.91 ± 0.31
13	2.37 ± 0.14	0	1.28 ± 0.10	1.67 ± 0.14	2.58 ± 0.12
9	2.71 ± 0.21	1.28 ± 0.10	0	1.64 ± 0.10	2.53 ± 0.14
12	2.71 ± 0.15	1.67 ± 0.14	1.64 ± 0.10	0	2.3 ± 0.07
11	2.91 ± 0.13	2.58 ± 0.12	2.53 ± 0.14	2.3 ± 0.07	0

Table III. Average separation distances between individuals at Zoo C (including standard errors).

Zoo C							
Average distances							
(Meters)							
INDIVIDUALS	15	19	22	14	21	20	17
15	0	1.63 ± 0.07	1.88 ± 0.07	1.69 ± 0.10	1.69 ± 0.06	1.66 ± 0.06	1.61 ± 0.06
19	1.63 ± 0.07	0	1.29 ± 0.09	1.48 ± 0.11	1.47 ± 0.09	1.76 ± 0.07	1.45 ± 0.09
22	1.88 ± 0.07	1.29 ± 0.09	0	1.58 ± 0.13	1.65 ± 0.06	1.81 ± 0.05	1.62 ± 0.07
14	1.69 ± 0.10	1.48 ± 0.11	1.58 ± 0.13	0	1.51 ± 0.10	1.54 ± 0.08	1.48 ± 0.09
21	1.69 ± 0.06	1.47 ± 0.09	1.65 ± 0.05	1.51 ± 0.10	0	1.40 ± 0.09	1.19 ± 0.06
20	1.66 ± 0.06	1.76 ± 0.07	1.84 ± 0.05	1.54 ± 0.08	1.40 ± 0.098	0	1.43 ± 0.08
17	1.61 ± 0.06	1.45 ± 0.09	1.62 ± 0.07	1.48 ± 0.09	1.19 ± 0.07	1.43 ± 0.08	0
18	1.60 ± 0.05	1.02 ± 0.07	1.34 ± 0.05	1.46 ± 0.08	1.40 ± 0.07	1.56 ± 0.06	1.19 ± 0.07
16	1.77 ± 0.06	1.34 ± 0.07	0.91 ± 0.07	1.48 ± 0.11	1.47 ± 0.06	1.65 ± 0.05	1.44 ± 0.08

	18	16
15	1.60 ± 0.05	1.77 ± 0.06
19	1.02 ± 0.07	1.34 ± 0.07
22	1.34 ± 0.05	0.91 ± 0.07
14	1.46 ± 0.08	1.48 ± 0.11
21	1.40 ± 0.07	1.47 ± 0.06
20	1.56 ± 0.06	1.65 ± 0.05
17	1.19 ± 0.06	1.44 ± 0.08
18	0	1.12 ± 0.05
16	1.12 ± 0.05	0

Table IV. Average separation distances between individuals at Zoo D (including standard errors).

Zoo D				
Average distances				
(Meters)				
INDIVIDUALS	25	26	24	23
25	0	6.86 ± 0.37	8.94 ± 0.57	7.30 ± 0.37
26	6.86 ± 0.37	0	6.58 ± 0.33	4.64 ± 0.38
24	8.94 ± 0.57	6.58 ± 0.33	0	6.11 ± 0.44
23	7.30 ± 0.37	4.64 ± 0.38	6.11 ± 0.44	0

Table V. Average separation distances between individuals at Zoo E (including standard errors).

ZooE							
Average distances							
(Metres)							
INDIVIDUALS	34	31	27	29	35	33	32
34	0	8.02 ± 0.67	6.59 ± 0.59	9.30 ± 0.83	4.86 ± 0.41	5.60 ± 0.90	8.86 ± 0.75
31	8.02 ± 0.67	0	7.44 ± 0.62	6.8 ± 0.59	8.04 ± 0.61	10.68 ± 0.75	5.06 ± 0.61
27	6.59 ± 0.59	7.44 ± 0.62	0	6.90 ± 0.59	7.24 ± 0.70	9.32 ± 0.60	7.51 ± 0.59
29	9.30 ± 0.84	6.8 ± 0.59	6.9 ± 0.59	0	8.99 ± 0.85	11.18 ± 0.76	5.99 ± 0.60
35	4.86 ± 0.41	8.04 ± 0.61	7.24 ± 0.70	8.99 ± 0.85	0	7.86 ± 0.73	8.76 ± 0.85
33	5.60 ± 0.90	10.68 ± 0.75	9.32 ± 0.60	11.18 ± 0.76	7.86 ± 0.73	0	11.57 ± 0.76
32	8.86 ± 0.75	5.06 ± 0.61	7.51 ± 0.59	5.99 ± 0.60	8.76 ± 0.85	11.57 ± 0.76	0
36	5.17 ± 0.49	9.17 ± 0.72	7.17 ± 0.85	8.42 ± 0.83	4.74 ± 0.30	8.5 ± 0.79	8.04 ± 0.58
37	8.55 ± 0.61	7.65 ± 0.51	7.91 ± 0.57	6.49 ± 0.49	8.55 ± 0.67	10.92 ± 0.78	6.09 ± 0.18
28	6.77 ± 0.72	8.60 ± 0.55	5.22 ± 0.47	7.33 ± 0.64	6.94 ± 0.75	9.19 ± 0.72	7.08 ± 0.56
30	8.50 ± 0.75	7.65 ± 0.58	7.83 ± 0.56	4.99 ± 0.50	8.23 ± 0.77	10.56 ± 0.82	6.41 ± 0.35

	36	37	28	30
34	5.17 ± 0.49	8.55 ± 0.61	6.77 ± 0.72	8.50 ± 0.74
31	9.17 ± 0.71	7.65 ± 0.51	8.60 ± 0.55	7.65 ± 0.57
27	7.17 ± 0.85	7.91 ± 0.57	5.22 ± 0.47	7.83 ± 0.56
29	8.42 ± 0.83	6.49 ± 0.49	7.33 ± 0.64	4.99 ± 0.50
35	4.74 ± 0.30	8.55 ± 0.67	6.94 ± 0.75	8.23 ± 0.77
33	8.5 ± 0.79	10.92 ± 0.78	9.19 ± 0.72	10.56 ± 0.82
32	8.04 ± 0.58	6.09 ± 0.17	7.08 ± 0.56	6.41 ± 0.35
36	0	6.56 ± 0.69	5.85 ± 0.52	6.82 ± 0.70
37	6.56 ± 0.69	0	7.20 ± 0.63	5.73 ± 0.33
28	5.85 ± 0.52	7.20 ± 0.63	0	5.53 ± 0.78
30	6.82 ± 0.70	5.73 ± 0.33	5.53 ± 0.78	0

Appendix 5

Photographs representing three of the environmental factors that may influence the behaviour of captive lion-tailed macaques.

Plates 1 and 2. Examples of variation in enclosure size

Plate 1 Small enclosure (Zoo B)

Plate 2 Large enclosure (Zoo A)

Plates 3 and 4. Examples of variation in enclosure complexity

Plate 3 Least complex (Zoo B)

Plate 4 Most complex (Zoo C)

Plates 5 and 6. Examples of variation in foraging substrate

Plate 5 Occasional foraging material provided (Zoo B)

Plate 6 Foraging material permanently provided (Zoo A)